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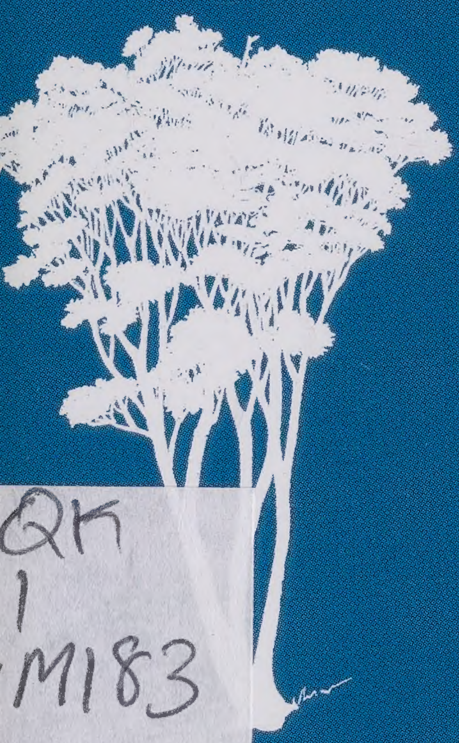

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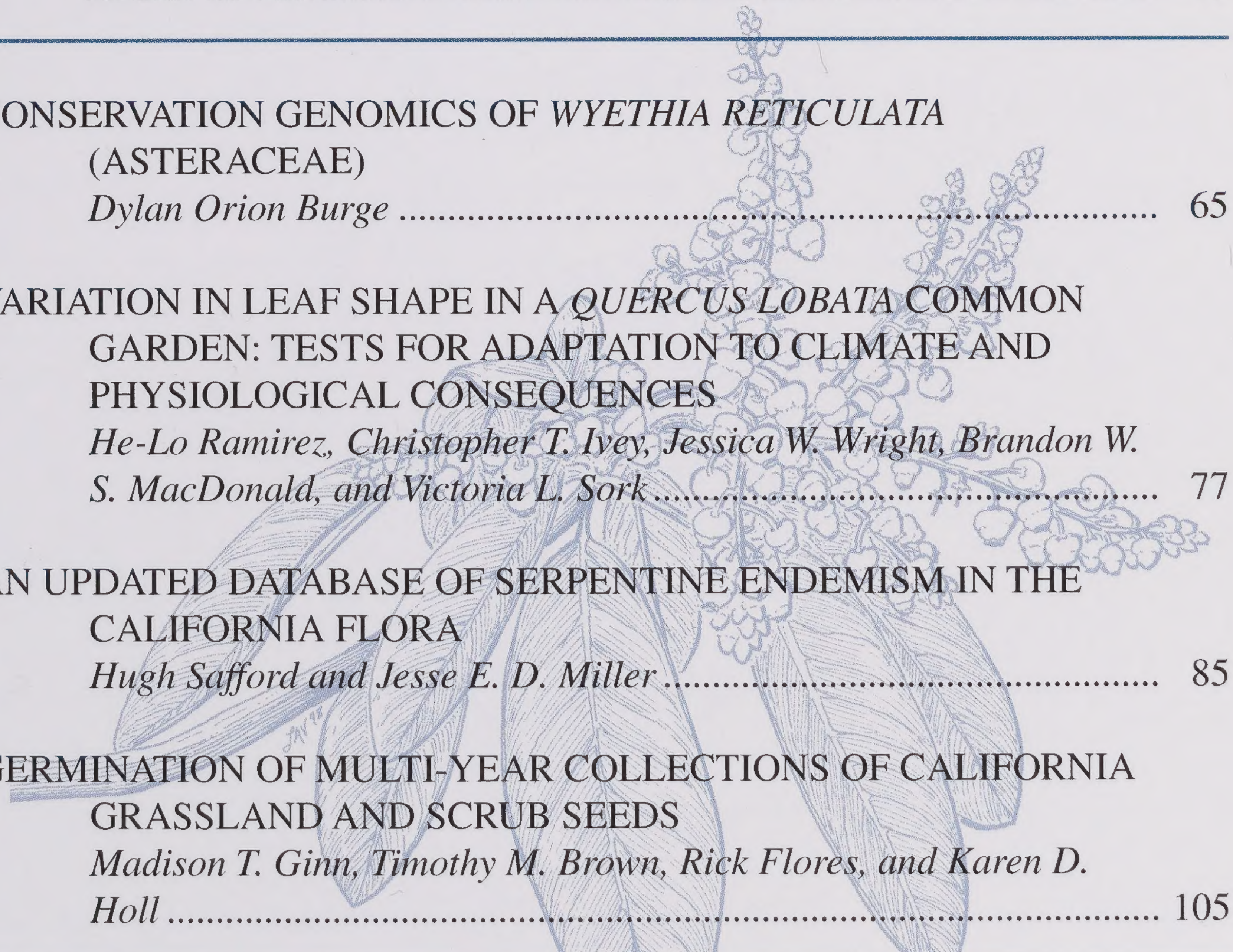

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NOTEWORTHY COLLECTION

CALIFORNIA

ISOETES MINIMA A.A.Eaton (ISOETACEAE).—Modoc Co., Modoc National Forest, Warner Mts, Dismal Swamp area, 0.5 mi S of Oregon state line; 41.9911°, -120.1645°; 2187 m; wet soil with short vegetation in a seasonal seepage area; 30 Jun 2018, *Duncan Thomas 13332 with Wendy Madar* (UC).

Soil around the plants contains numerous megaspores from last year, with long blunt spines; *I. nuttallii* A.Braun ex. Engelm. megaspores lack spines.

Previous knowledge. Isoetes minima was described by Eaton (1898) from Spokane County, Washington collections made by Wilhelm Suksdorf. Later authors tended to treat it as a variety of *Isoetes howellii* Engelm., a widespread species found throughout the West Coast states (Pfeiffer 1922; Taylor et al. 1993). Based on molecular analyses, Taylor et al. (2001) re-elevated it to species status, while recent studies (Hoot et al. 2006; Larsén and Rydin 2016) revealed that instead of being closely related to *I. howellii*, *I. minima* is in a deeply divergent lineage and is most closely related to *I. nuttallii* and *I. orcuttii* A.A.Eaton, with which it shares the feature of three-lobed corms (*I. howellii* and relatives have bilobed corms; Pfeiffer 1922; Taylor et al. 1993; Freund et al. 2018). *Isoetes minima* was known only from the Suksdorf collections until new populations were discovered by A. Ceska in Washington and British Columbia (Ceska and Ceska 2001).

There are no herbarium records attributed to *Isoetes minima s.s.*. in California in either of the California Consortium of Herbaria (CCH) databases (CCH1 and CCH 2, CCH 2019) or Consortium of Pacific Northwest Herbaria Specimen Database (CPNH 2019). There is a single specimen attributed to *I. howellii* var. *minima* from 1896 in CCH (2019; Record: SEINET10754764), yet, upon examination of a digital image of the specimen, none of the annotation labels ascribe it to *I. howellii* var. *minima*, only to *I. howellii*, so this is likely an error in the database. From the Washington Natural Heritage Program (WNHP 2005), *I. minima* is only found in two counties of Washington state and one site in southern British Columbia. Recent collections have extended its known range to western Idaho (Washington Co.), northeastern Oregon (Wallowa, Baker, Umatilla, and Union cos.), southeastern Oregon (Warner Mountains of Lake Co.), Washington east of the Cascade Range (Kittitas, Okanogan, and Columbia cos.), with additional sites in southern British Columbia. However, known populations are widely scattered across the range and few in number (CPNH 2019). In both Washington and Oregon, *I. minima* is considered a taxon of concern: S1 in Washington (Critically imperiled; WNHP 2005; CPNH 2019), and Category 1 in Oregon (threatened/endangered throughout range; Oregon Biodiversity Information Center 2019).

Isoetes minima, like *I. nuttallii*, is a terrestrial to partially amphibious species. According to Eaton (1898) and WNHP (2005), the taxon is found in damp sagebrush prairie areas, and it also occurs in seeps and seasonally mesic-to-hydric meadows (CPNH 2019). This habitat is similar to that of *I. nuttallii*, but the two species are geographically isolated: *I. minima* has only been found east of the Cascade Range along the margins of the Columbia Plateau and Great basin Desert, whereas *I. nuttallii* is found west of the Cascades of Oregon and Washington, and the Sierra Nevada and Peninsular Range of California.

Significance. This collection represents a range extension for *I. minima* and is the only record from California (CCH 2019; CPNH 2019; Jepson Flora Project 2019; The University and Jepson Herbaria 2019). A second collection was made 8.4 miles north of the site of this on (DT 13331, 5/30/2018, OSC deposition pending) in the Warner Mountains on the Oregon side of the state line. This is a considerable range expansion, as the nearest known site is near Baker City (245 miles) and represents an extension of the southern range of the species by 170 miles.

Additional comments. There are contradicting accounts of the coloration of the spores in this species. The WNHP (2005) describe the megaspores of *I. minima* as white, whereas Thomas (2015) notes that they are black when wet and light gray when dry. The megaspores from the Dismal Swamp plants are off-white to medium-gray in color, but dark gray, nearly black when wet, yet otherwise fit the description provided. It is possible that the coloration of the spores is variable across the species' range.

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LITERATURE CITED

CESKA, A. AND O. CESKA. 2001. *Isoetes minima* A.A.Eaton (Isoetaceae): an overlooked terrestrial quillwort of the Pacific Northwest. Botanical Electronic News (BEN) 269:http://www.ou.edu/cas/botany-micro/ben/ben269.html.

CCH (eds.). 2019. Data provided by the participants of the Consortium of California Herbaria. Website: ucjeps.berkeley.edu/consortium/ [accessed 01 October 2019]

CPNH (eds.). 2019. Consortium of Pacific Northwest Herbaria Specimen Database. University of Washington Herbarium, Seattle, WA. Website: http://www.pnwherbaria.org [accessed 30 September 2019].

Eaton, A. A. 1898. *Isoetes minima.* Fern Bulletin 6:30.

Freund, F. D., W. A. Freyman, and C. J. Rothfels. 2018. Inferring the evolutionary reduction of corm lobation in *Isoetes* using Bayesian model-averaged ancestral state reconstruction. American Journal of Botany 105:275–286.

Hoot, S.B., W.C. Taylor, and N.S. Napier. 2006. Phylogeny and biogeography of *Isoetes* (Isoetaceae) based on nuclear and chloroplast DNA sequence data. *Systematic Botany* 31: 449–460.

Jepson Flora Project (eds.) 2019. Jepson eFlora. Website: http://ucjeps.berkeley.edu/eflora/ [accessed 30 Septemer 2019].

Larsén, E. and C. Rydin. 2016. Disentangling the phylogeny of *Isoetes* (Isoetales), using nuclear and plastid data. International Journal of Plant Sciences 177:157–174.

Oregon Biodiversity Information Center. 2019. Rare, threatened and endangered vascular plant species of Oregon. Oregon Biodiversity Information Center, Portland State University, Portland, OR. April 2019. https://inr.oregonstate.edu/sites/inr.oregonstate.edu/files/2019-rte-vascs.pdf

Pfeiffer, N. E. 1922. Monograph of the Isoetaceae. Annals of the Missouri Botanical Garden 9:79–233.

Taylor, C. W., N. T. Luebke, and A. R. Lekschas. 2001. Taxonomic status and evolutionary relationship of *Isoetes minima* A.A.Eaton (Isoetaceae) based on nuclear ribosomal DNA internal transcribed spacer sequences. Botanical Electronic News (BEN) 304:http://www.ou.edu/cas/botany-micro/ben/ben304.html

Taylor, C. W., N. T. Luebke, D. M. Britton, R. J. Hickey, and D. F. Brunton. 1993. Flora of North America eFloras 2 Website: http://betafloranorthamerica.org/Iso%C3%ABtes [accessed 20 September 2019].

The University and Jepson Herbaria (eds.) 2019. University and Jepson Herbaria, University of California, Berkeley, CA. Website: http://ucjeps.berkeley.edu/ [accessed 30 September 2019].

Thomas, D. 2015. Isoëtaceae. Pp. 79–81 *in* S. C. Meyers, T. Jaster, K. E. Mitchell, L. K. Hardison (eds). Flora of Oregon Vol. 1: Pteridophytes, Gymnosperms and Monocots. BRIT Press, Fort Worth, TX.

WNHP (eds). 2005. Washington Natural Heritage Program, Washington Dept. of Natural Resources. Website: https://www.dnr.wa.gov/publications/amp_nh_isomin.pdf?pbnuea [accessed 30 September 2019].

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CONSERVATION GENOMICS OF *WYETHIA RETICULATA* (ASTERACEAE)

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Abstract

Wyethia reticulata Greene is a rare perennial herb found only on gabbro-derived soils of the Pine Hill formation in the Sierra Nevada foothills of El Dorado County, CA. *Wyethia reticulata* is capable of both vegetative (clonal) and sexual reproduction, although the former is thought to be more common than the latter, with sexual reproduction tied to fire. The potential dominance of vegetative reproduction has conservation implications for *W. reticulata*, as populations could appear healthy in terms of stand density, while losing genetic diversity due to a lack of sexual recruitment. Past genetic assessments of *W. reticulata* relied on low-resolution markers from a small number of populations and did not directly address conservation issues. Here, double-digest random amplified DNA (ddRAD) sequencing was used to develop a high-resolution genomic dataset for a sample of 168 *W. reticulata* samples from seven locations that represent every known population center of the species. The data was used to 1) calculate the frequency of asexual reproduction, 2) determine which populations contain unique genetic variation, and 3) test whether there are any ecological correlates of genetic patterns. In contrast to past genetic research, the results presented here indicate that clonality is not common; less than 2% of plants were identified as being derived from asexual reproduction. Nevertheless, some locations seem to be more affected by asexuality than others; the index of association varied from 4.4 to 19.4 ($\bar{M} = 10.9$). Genetic differentiation among locations was low ($F_{st} = 0.03$-0.04). However, clustering identified three distinct population segments that were not previously recognized. Elevation was the only environmental variable significantly associated with genetic differentiation. Based on these results, it is recommended that conservation effort be focused on genetically isolated population segments.

Key Words: California, clonal, ddRAD, DNA, endemic, genet, Pine Hill, ramet.

Wyethia reticulata Greene (El Dorado County mule ears), is a rare, diploid (2n=38), perennial herb found in the Pine Hill region of El Dorado County, California. It occurs only on soil derived from gabbro rock of the Pine Hill Formation (Wilson 1986; Hunter and Horenstein 1991; Wilson et al. 2009). *Wyethia reticulata* is a California Native Plant Society (CNPS) listed plant (California Rare Plant Rank 1B.2; CNPS 2019) and a US Fish and Wildlife Service Species of Concern (USFWS 2002). It is one of eight rare plants associated with gabbro-derived soils of the Pine Hill area, a region known for elevated plant endemism (Wilson et al. 2009).

Wyethia reticulata is known for its ability to reproduce asexually via rhizomes (Ayres 1997; Ayres and Ryan 1997; USFWS 2002). In this mode of reproduction, each seedling can form a group of genetically identical individuals (hereafter referred to as a genet) in which all of the stems (hereafter referred to as ramets) are genetically identical. It is not known how frequently sexual versus asexual reproduction occurs in populations of *W. reticulata*, but mass-flowering of colonies and recruitment of seedlings seems to be associated with fire or mechanical disturbance (Ayres 1997). Nevertheless, recruitment is low even after disturbance (Ayres 1997), meaning that the population biology of this species may be strongly affected by the long-term persistence of genets. This idea is supported by past molecular work using RAPDs combined with allozymes (Ayres and Ryan 1997, 1999). These studies suggest that although the analyzed populations are dominated by a few genets, there is high genetic diversity among populations (Ayres and Ryan 1997), even compared to a sympatric congener that is thought to have a lower rate of asexual reproduction (Ayres and Ryan 1999). These results are thought to be consistent with a species in which the persistence of large, asexual colonies results in the genetic divergence of populations.

Although *W. reticulata* co-occurs with two other species of *Wyethia* (*Wyethia bolanderi* [A.Gray] W.A.Weber and *W. angustifolia* [DC.] Nutt.), both of which have the same ploidy as *W. reticulata*, neither of these species is a close relative (Moore and Bohs 2003). What is more, in the Pine Hill region *W. bolanderi* flowers in early spring and *W. angustifolia* in late spring, while *W. reticulata* does not begin to flower until the summer (Keil 2012), which means that opportunities for genetic exchange are limited. Although neither *Wyethia* species that occurs with *W. reticulata* is a close relative, three closely related congeners do occur in California (Moore and Bohs 2003), including *Wyethia elata* H.M.Hall, the sister species of *W. reticulata*. However, these species are found farther south, the nearest population being at least 100 km south of Pine Hill (Keil 2012). Thus, it is unlikely that genetic exchange with other *Wyethia* species is relevant to the population genetics of the focal species. This idea is supported by RAPD and allozyme data, which failed to detect any evidence of genetic exchange (Ayres and Ryan 1999).

Throughout its limited geographic range, *W. reticulata* is under threat from development, fire suppression, illegal dumping, and off-highway vehicle use, which have led to loss of some populations and fragmentation of others (CNPS 2019). As outlined above, past genetic research has suggested that there is a low rate of sexual reproduction in the species, with recruitment from seeds taking place mainly in the immediate aftermath of fire or other disturbance (Ayres 1997). This aspect of the species' ecology makes it especially vulnerable to habitat fragmentation and fire suppression; in small, isolated areas of habitat the populations could become dominated by just a few genets. In this case, a population might appear healthy, with high stem density in the habitat, despite a lack of genetic diversity. It is also known that *W. reticulata* is self-incompatible and depends on bees to facilitate pollen transfer (Ayers 1997). In isolated populations dominated by a few genets, sexual reproduction might fail due to a lack of pollen donors. Finally, variation in ecological conditions across the small, but topographically complex, Pine Hill region may have driven the evolution of associations between genetics and environment (Baack et al. 2015). Such associations may help populations to survive in their environment, but could also lead to barriers to geneflow (Baack et al. 2015) that might curtail the spread of beneficial genetic variation.

To develop and implement a conservation strategy for any rare species, there is a need for high-resolution information on genetic patterns both within and among populations (Allendorf et al. 2010). Past genetic research on *W. reticulata* yielded important insights into population genetic patterns in this species using RAPDs and allozymes (Ayres and Ryan 1997, 1999). However, this work focused on just four populations, relied on markers with a much lower power of resolution than is possible with direct DNA sequencing, and did not directly address conservation concerns. In the more than 20 years that have elapsed since the publication of these studies, the advent of high-throughput DNA sequencing has made it feasible to develop high-resolution datasets for a large number of samples of any species based on direct DNA sequencing (Mardis 2017).

Here, restriction-associated DNA (RAD) sequencing (Davey et al. 2013) is used to develop a large, single nucleotide polymorphism (SNP) dataset for all major population centers of *W. reticulata* (Fig. 1). These genetic data are used to estimate population genetic parameters and to determine: 1) the species-wide extent of clonal reproduction, 2) which populations are most genetically isolated and/or depauperate, and 3) whether the populations are adapted to local climatic conditions. Based on these analyses, recommendations are made for conservation.

MATERIALS AND METHODS

Sampling

For sampling of *W. reticulata*, seven locations in the Pine Hill area were selected (Table 1, Fig. 1). Locations were selected to represent every major population center of the species and the range of environmental conditions under which the species is found. Locations were selected based on information obtained during preliminary visits to known population centers carried out between 15 and 19 June 2018. Preliminary visits allowed the author to select large populations within which to implement the sampling scheme outlined below.

To prevent confusion between populations and subpopulations, collecting locations are referred to as 'locales.' Locales are spatially discontinuous groups of plants with centers at least 1000 m apart and edges at least 100 m apart. Sampling was carried out using a spatially explicit, repeatable approach based on past research into the population biology of *W. reticulata* (Ayres and Ryan 1997) and a recent review of best practices for population genetic sampling of plants with mixed clonal and sexual reproduction (Arnaud-Haond et al. 2007), such as *W. reticulata*

Ayres and Ryan (1997) sampled three contiguous patches of *W. reticulata* with a total area of 900 m^2 and identified a total of 9 genets in this area; this implies that on average, there is one genet present in a 100 m^2 patch, meaning that in an area of continuous cover, genets are separated, on average, by 5.6 m (the radius of a circle with an area of 100 m^2). Ayres and Ryan (1997) also found significant genetic differentiation among populations separated by as little as 500 m. Based on this existing information for the focal species, a modification of the stratified random sampling design recommended by Arnaud-Haond et al. (2007) was used, as this method was developed for species with patchy cover. A custom R script (version 3.6.2; R Development Core Team, R Foundation for Statistical Computing, Vienna, Austria) written by the author was used to obtain 48 random GPS points for each locale; the points were at least 5.6 m apart inside a 300 m square. During a locale visit, each of the GPS points was visited. At some locales, visits to the points required the use of protective clothing and knee pads in order to access plants and avoid injury from the dense chaparral. If a colony was present at a point, a sample was obtained there. This continued until all 48 points were visited. If the 48 points yielded less than 24 samples, the points were re-visited in random order, and the nearest colony sampled, selecting a stem at least 5.6 m distant from the nearest sampled stem. This was continued until 24 samples were obtained. At locales other than Square Nail (Table 1, Fig. 1), this strategy yielded sufficient samples without difficulties. Due to the small number of plants at the Square Nail Locale, most of which were associated with a disused fire road (Fig. 1), an

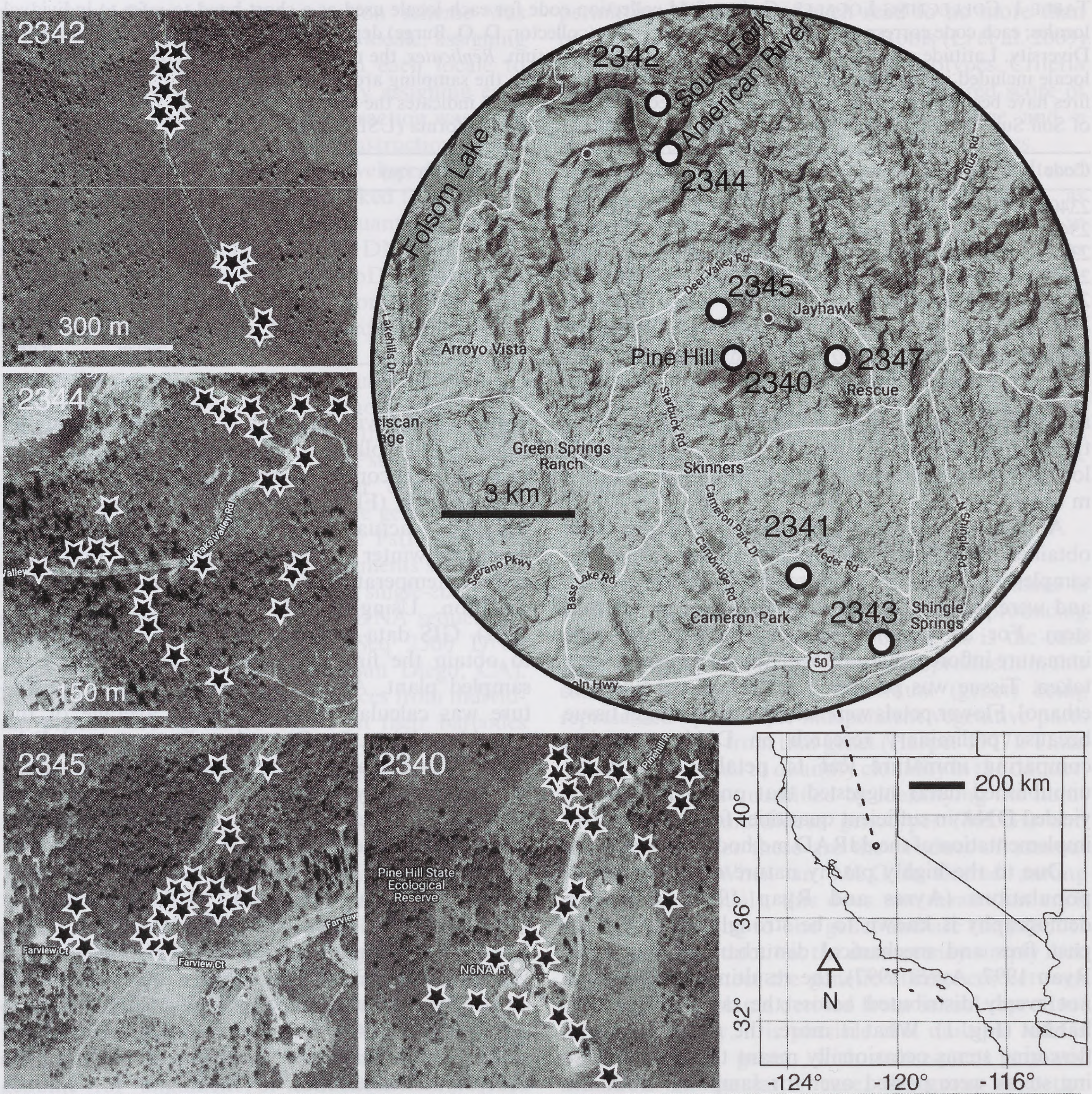

FIG. 1. Sampling map for *Wyethia reticulata*. Grid dimensions are in degrees of latitude and longitude (WGS84 datum). Scale bar for locale 2344 applies to all locales other than 2342. See Table 1 for more information on locales.

TABLE 1. COLLECTING LOCALES. *Code*, a field collection code for each locale used as a short-hand to refer to individual locales; each code corresponds to an herbarium voucher (collector: D. O. Burge) deposited at the UC Davis Center for Plant Diversity. Latitude and longitude are given in the WGS 84 datum. *Replicates*, the number of biological replicates from this locale included in sequencing. *Fire*, the date of the last fire within the sampling area of the locale; 'never' indicates that no fires have been known to occur at the locale in recorded history. *Soil*, indicates the soil type at the locale, from examination of Soil Survey Geographic (SSURGO) data for El Dorado Area, California (USDA 2019).

Code	Locale name	Latitude	Longitude	Elevation (m)	Replicates	Fire	Soil
2340	Pine Hill	38.7210	-120.9898	605	3	Never	RgE2
2341	Cameron Park	38.6766	-120.9716	480	3	Never	RgE2
2342	Square Nail	38.7726	-121.0089	320	3	Never	RgE2
2343	Ponderosa	38.6622	-120.9524	460	3	2007	RfC
2344	Weber Creek	38.7617	-121.0066	200	4	1964	RgE2
2345	Farview	38.7317	-120.9945	485	3	Never	RfE
2347	Tiffany Hill	38.7219	-120.9604	450	3	Never	RgE2

additional eight stems were sampled to the south of the originally targeted area (Fig. 1); samples at this location were haphazardly selected, no less than 5.6 m apart.

At each locale, up to four duplicate samples were obtained to be used as biological replicates. Duplicate samples were obtained from randomly selected stems, and were taken from the same inflorescence on that stem. For all samples, ligulate petals of a single immature inflorescence (anthers not yet dehisced) were taken. Tissue was preserved in two mL of absolute ethanol. Flower petals were selected as the target tissue because preliminary research on DNA extraction comparing immature leaf to petal tissue (Burge unpublished data) suggested that only flower petals yielded DNA in sufficient quantities for the successful implementation of the ddRAD method employed here.

Due to the highly patchy nature of *W. reticulata* populations (Ayres and Ryan 1997), in which demography is known to be strongly influenced by past fires and mechanical disturbance (Ayres and Ryan 1997, Ayres 1997), the resulting samples were not evenly distributed across the targeted areas of habitat (Fig. 1). What is more, the requirement for flowering stems occasionally meant that non-flowering stems were passed over for sampling. Both the location and flowering status of stems can be affected by both fire and mechanical disturbance history (Ayres and Ryan 1997; Ayres 1997). However, other than fire history at a locale (see below), the influence of non-random historical factors such as mechanical disturbance was not considered in the sampling due to the difficulty of measuring and quantifying such disturbances. For example, at the Square Nail locale few plants were found, even under chaparral that had re-grown since a prescribed fire that burned in 1990 (Ayres 1997); nearly all plants (flowering or not) located during extensive visits to the area prior to sampling were located within 10 m of the fire road (Burge unpublished data; Fig. 1).

Environmental Data

Climate and soil data for each sampled plant were inferred for use in tests of association between genetics and environment (see Association Analysis, below). The following six climatic variables were selected to encompass important drivers of vegetation patterns (Flint et al. 2013): 1) climatic water deficit, 2) actual evapotranspiration, 3) average minimum winter temperature, 4) average maximum summer temperature, 5) annual precipitation, and 6) elevation. Using the R package *raster* (Hijmans 2017), GIS data from Flint et al. (2013) were used to obtain the first five climatic variables for each sampled plant. Average minimum winter temperature was calculated by taking the average of the monthly minima for December, January, and February. The average maximum summer temperature was calculated by taking the average of the monthly maxima for June, July, and August. Climatic water deficit and actual evapotranspiration are described by Hijmans (2017). Elevation was taken using a Garmin 12 GPS unit (Garmin Ltd., Olathe, Kansas).

Soil data was taken from GIS data layers in the Soil Survey Geographic (SSURGO) database for El Dorado Area, California (USDA 2019). For each locale, the map unit name (MUNAME) for the soil type underlying the area was recorded. For all raw environmental data, see Appendix S1 (doi.org/10.5061/dryad.n02v6wwt2).

Information on past fires was obtained from the CAL FIRE Resource Assessment Program Fire Perimeters (FRAP 2019), which contains data on all fires of greater than ten acres in the state of California. The data covers all such fires since 1898. If a fire burned all or part of the locale, the date of the fire was recorded. For fires smaller than ten acres, records maintained by the Motherlode Field Office of the Bureau of Land Management were examined; no such fires recorded by the office had affected the targeted sampling areas.

DNA Extraction and Sequencing

Genomic DNA was extracted from the flower petals by Eurofins BioDiagnostics (River Falls, Wisconsin) using the LGC sbeadex 96 well plant kit. Two kits were used. In order to avoid systematic DNA-quality biases among locales based on extraction, a blocking and randomization scheme was employed. Samples were blocked by locale, assigning equal numbers of individuals from each locale to each of the kits, and then randomly assigning each individual to a well within a kit. Extraction was done according to the manufacturer's instructions, with several proprietary modifications developed by Eurofins BioDiagnostics. DNA was checked for degradation using a 1% agarose gel, and quantified using a spectrophotometer. Total genomic DNA was standardized to 30 ng/μL by Eurofins BioDiagnostics and sent directly to Floragenex, Inc. (Portland, Oregon) for further quality control, library construction, and DNA sequencing.

The library preparation and sequencing methods employed by Floragenex followed those described by Lozier (2014), with the exception that the present work used the restriction enzyme PstI (Hipp et al. 2014). In brief, sequence identifier barcodes and sequence adapters were added to the genomic DNA after digestion by the endonuclease PstI. Barcoded samples were combined and the fragments sequenced outwards from restriction-sites using single-end DNA sequencing reads 100 bp long. All DNA sequencing was done using a run of a HiSeq 2500 DNA sequencing instrument (Illumina, San Diego, CA). Following sequencing, DNA sequences from individual plants were separated based on their barcodes using the program fastq-multx (Aronesty 2013); the barcodes were then removed from the sequences.

Variant Detection

Due to the lack of an existing reference genome for *Wyethia* or a closely related member of Asteraceae, detection of variation among individual plants was done using a 'RAD reference' approach (Lozier 2014), in which a kind of reference genome was constructed using sequence data from the plant with the greatest number of unique RAD clusters. We employed this strategy to ensure the best reference genome for alignment of sequences from other individuals. The plant selected for use as the reference was 2344-22 (Table 1; Appendix S1, doi. org/10.5061/dryad.n02v6wwt2). In developing the RAD reference, custom methods developed by Floragenex were used to cluster identical sequences that had 5-500× sequencing coverage (Lozier 2014), which produced a preliminary assembly. The assembly was then collapsed back to separate sequences and these sequences were realigned against the preliminary RAD reference genome using the program BWA (Li and Durbin 2009), allowing at most four mismatches among reads within a cluster. The purpose of self-alignment was to identify and remove repetitive DNA regions.

Reads for each individual plant were aligned to the RAD reference using BOWTIE (Langmead et al. 2009), relying on sequence quality information to aid in the process of match-making, allowing a maximum of three mis-matched bases per read, and permitting alignment of each read to no more than one region of the reference. SAMtools (Li et al. 2009) was used to detect SNPs and call genotypes. Criteria for SNP calling required a minimum phred score of 10, a minimum of 6× sequence coverage and a maximum of 25% missing data across samples.

Following SNP calling, the data were filtered based on the repeatability of genotype calls, as revealed by the 22 biological replicates included in the sequencing and SNP calling. Each of the loci was checked for genotype concordance between replicates. A locus was removed when the biological replicates had different genotype calls. Such discordant loci were removed in order to ensure that only repeatable loci were included in the final dataset. The process of identifying and removing discordant loci was carried out using a proprietary bash script (Floragenex, Inc.) that employed VCFtools (Danecek et al. 2011).

Quantification of Clonality

Previous research indicated that *W. reticulata* is strongly clonal (Ayres and Ryan 1999), reproducing asexually via underground rhizomes. As is the case with all organisms capable of clonal reproduction, this can lead to one genetic individual (genet) being represented by multiple independent vegetative parts (ramets) derived from that genet (Harper 1977). Thus, an effort was made to quantify clonality in the dataset.

Clonality was quantified by identifying the number of unique multilocus genotypes (MLGs) and assessing whether these are the product of asexual reproduction. When an MLG is shared among multiple individuals, this does not mean that such individuals belong to one genet and are the product of asexual reproduction; the dataset may simply lack the power to detect the genetic differences between closely related plants derived from sexual reproduction. Conversely, it is possible that multiple MLGs belong to one genet, with subsequent somatic mutation. In the latter case, the group is better referred to as a multilocus lineage, or MLL. Overall, the definition of MLLs relies on selection of a genetic distance threshold to group MLGs into MLLs (reviewed by Bailleul et al. 2016). Some researchers have solved this problem by collecting genetic data on known ramets in order to directly quantify the amount of genetic differentiation expected among ramets (Douhovnikoff and Dodd 2003). However, such studies are very rarely done due to the logistical hurdles involved. More frequently, workers have relied on the following categories of methodology to group MLG: 1) clustering algorithms (Kamvar et al. 2015), 2) modeling asexual versus sexual reproduction (Bailleul et al. 2016), 3) visual examination of frequency distributions of genetic distance (Meirmans and Van Tienderen 2004; Arnaud-Haond and Belkhir 2007; Clark and Jasieniuk 2011), and 4) various combinations of these methods. In all such methods, however, the definition of MLLs depends,

TABLE 2. POPULATION GENETIC SUMMARY STATISTICS. *Code*, a field collection code for each locale used as a short-hand to refer to individual locales; each code corresponds to an herbarium voucher (collector: D. O. Burge) deposited at the UC Davis Center for Plant Diversity. *Alleles*, refers to the number of alleles inferred to segregate in each locale. *Heterozygosity*, Nei's expected heterozygosity (Nei 1978). I_A, index of association (Smith et al. 1993). $\bar{r}_d$, Index of multi-locus linkage disequilibrium (Agapow and Burt 2001). Latitude and longitude are in the WGS84 Datum.

Code	Locale name	Alleles	Heterozygosity	I_A	$\bar{r}_d$
2340	Pine Hill	7279	0.020	12.71	0.011
2341	Cameron Park	7394	0.022	4.37	0.003
2342	Square Nail	7117	0.019	8.96	0.009
2343	Ponderosa	7185	0.020	8.79	0.008
2344	Weber Creek	7100	0.019	19.40	0.020
2345	Farview	7093	0.019	16.15	0.016
2347	Tiffany Hill	7475	0.022	5.77	0.004

either directly or indirectly, on assumptions made by the user.

Methods to quantify clonality in the present study were selected to minimize the number of assumptions, especially with respect to population genetic or demographic parameters that were not directly measured. First, the R package *poppr* v. 2.8.3 (Kamvar et al. 2014) was used to group MLGs into MLLs based on a-priori selection of a genetic distance threshold. A Euclidean distance matrix was created using the *bitwise.dist* function of *poppr*. The *filter_stats* algorithm was then applied to this matrix under default parameters, identifying three alternative genetic distances thresholds that could be used to identify MLLs. Requiring a minimum genetic distance to distinguish one MLL from another allows for small differences among MLGs, such as those derived from DNA sequencing error or somatic mutations. The *mlg.filter* option of *poppr* was used, under default settings, to collapse MLGs into MLLs based on each of the three genetic distance thresholds, *farthest_neighbor* (merges MLGs based on maximum distance between individuals in either of the clusters; most strict), *average_neighbor* (merges MLGs based on average distance between every pair of individuals between clusters; intermediate strictness), and *nearest_neighbor* (merges MLGs based on minimum distance between individuals in either cluster; least strict). Results of the three methods were similar: *farthest_neighbor* identified one MLL represented by six individuals from four locales (2340, 2343, 2344 & 2345); *average_neighbor* identified one MLL represented by five individuals from three locales (2343, 2344, & 2345); *nearest_neighbor* identified two MLLs represented by four individuals from three locales (2343, 2344, & 2345). To test sensitivity to the genetic distance methods used, the analysis was run again using dissimilarity distance (*diss.dist* in *poppr*) and Nei's genetic distance (*nei.dist* in *poppr*). The results were identical.

The R package *RClone* v. 1.0.2 (Bailleul et al. 2016) was used as a graphical means to identify MLLs, and thereby separate ramets from genets among the sampled stems. The pairwise allele distances among the sampled stems were calculated (*genet_dist* function of *RClone*) and plotted as histograms for each local. As in Meirmans and Van Tienderen (2004) and Clark and Jasieniuk (2011), it was assumed that the frequency distributions of pairwise distances would each contain a wide valley separating stems derived from asexual reproduction (low end of the frequency distribution) from those derived from sexual reproduction (high end). However, no such valley was identified for any locale; in all cases, the major cluster began at an allele distance of more than 1000 (Appendix S2, doi.org/10.5061/dryad.n02v6wwt2). As in Meirmans and Van Tienderen (2004), this cluster of greater distances was inferred to belong to the group of samples derived from sexual reproduction; additional clusters were present in some histograms, but these were at greater distances. Overall, the graphical results were taken to indicate that no stems were derived from clonal reproduction; such asexual reproduction would be expected to result in a separate cluster of allele distances at the low end of the distribution (Meirmans and Van Tienderen 2004; Clark and Jasieniuk 2011), which was not observed.

As a final alternative method of inferring the degree to which plants are reproducing asexually, the index of association (I_A, Smith et al. 1993) and the index of multi-locus linkage disequilibrium ($\bar{r}_d$, Agapow and Burt 2001) were inferred for each population. Calculations were done in *poppr* (Kamvar et al. 2014). Both these indices express linkage disequilibrium. As such, both tend to be higher in populations where there is a higher level of asexual reproduction. The I_A index is similar to $\bar{r}_d$, but the latter accounts for the number of loci sampled, while the former does not. Both of the indices suggest that asexual reproduction is taking place mainly in locales 2340, 2344, and 2345 (Table 2). This supports the results of the MLG-based analyses above, which identified a small number of potential clones from some of the same locales.

Although the indices of association indicate that asexual reproduction may be taking place in some locales (Table 2), the MLL results suggest that nearly every sampled plant is a separate genetic individual. Thus, it appears that asexual reproduction (clonality) is not common in *W. reticulata*, at least at the scale (above 5.6 m horizontal distance) that sampling was done. Given the low rate of clonality (only two MLLs identified using the least conservative filtering algorithm of *poppr*; less than 1.2% of samples), asexual reproduction was ignored in subsequent population genetic analyses; all of the work described below was carried out on the complete dataset (168 samples; Table 1), excluding the biological replicates

Genetic Differentiation Among Locales

Population genetic analysis was used to obtain genetic diversity statistics for each locale and to estimate the amount of differentiation among locales. The R packages *adegenet*, v. 1.3-1 (Jombart 2008; Jombart and Ahmed 2011) and *poppr*, v. 2.8.0 (Kamvar et al. 2014, 2015) were used to calculate population genetic statistics. The package *adegenet* was used to calculate allelic diversity and heterozygosity for each locale. Differentiation (F_{st}) among locales was calculated using the *pairwise.fst* algorithm of the R package *hierfstat* (Goudet 2005). The significance of differentiation was tested using Goudet's G-statistic Monte Carlo test, which was implemented in *adegenet* with 500 replicates (Jombart 2008). Isolation by distance at the level of the locale was assessed using partial Mantel tests carried out in the R package *vegan* v. 2.5-1 (Dixon 2003), controlling for the latitude and longitude of the locale centroid (Table 1); Pearson and Spearman correlation coefficients were used with 1000 replicates of the permutation test. As an additional means to quantify the relationship between genetics and spatial distance, the R package *EcoGenetics* v 1.2.1-5 was used to test for spatial autocorrelation; the *eco.malecot* algorithm was implemented, testing for global autocorrelation between great circle distance and kinship (Nason's F_{ij}; Loiselle et al. 1995)

Clustering Analysis

The program STRUCTURE, v. 2.3.4 (Pritchard et al. 2000; Falush et al. 2003, 2007; Hubisz et al. 2009) was used to cluster the sampled individuals. 100,000 Markov chain Monte Carlo (MCMC) replicates were run, discarding 20,000 replicates as burnin (Hubisz et al. 2009). The analysis was repeated eight times, varying K (the number of theoretical clusters) from one to eight, with 10 MCMC replicates at each K. The optimal K was inferred using STRUCTURE HARVESTER (Earl and vonHoldt 2012), according to the method of Evanno et al. (2005).

Association Analysis

Association between environment and genetics was tested using redundancy analysis (RDA; Forester et al. 2018). RDA was done using the R package *vegan* (Dixon 2003; Bourret et al. 2014). An R script developed by Forester et al. (2018) was used to impute missing genetic data. Unconstrained RDA was run on the resulting dataset to test for collinearity of the variables; all of the variables with a variance inflation factor greater than 10 (Oksanen et al. 2018) were removed, which left elevation, climatic water deficit (hereafter 'cwd') and actual evapotranspiration (hereafter 'aet'). A constrained RDA was then carried out, constraining on latitude and longitude. ANOVAs were run to test for the significance of the full model, the significance of each RDA axis, and the significance of each of the variables. In all cases, 100 replicates of the permutation test were used (Oksanen et al. 2018; Forester et al. 2018).

RESULTS

Genotypes

A total of 190 DNA samples were subjected to RAD sequencing, including 22 biological replicates (Appendix S1, doi.org/10.5061/dryad.n02v6wwt2). Quality was high for all samples; none were excluded due to low sequencing coverage or excessive missing data. Coverage averaged 5,536,301 reads per individual for the 190 samples (SD = 2,030,746). Raw DNA sequence data is at NCBI (BioProject accession PRJNA549276). A total of 14,013 SNP loci were called (Appendix S3, doi.org/10.5061/dryad.n02v6wwt2). Of these, 5,930 loci passed all filters. No additional filters were applied; the dataset contains 65 invariant loci (i.e., 98.9% of the loci are polymorphic). The filtered data is at the Dryad Digital Repository (Appendix S4, doi.org/10.5061/dryad.n02v6wwt2).

Environmental Conditions

Environmental conditions did not vary strongly across the locales (Table 1), despite the rugged nature of the terrain (Fig. 1). Elevation varied from 200 m at the Weber Creek locale, at the banks of the South Fork of the American River, to more than three times this altitude, at the summit of Pine Hill (602 m; Table 1). Average annual rainfall varied from 745 mm at the Weber Creek locale, 2344, to 817 mm at Cameron Park, 2341 (Table 1; Appendix S1, doi.org/10.5061/dryad.n02v6wwt2). The lowest climatic water deficit (cwd) was at Weber Creek (733 mm), and the highest at Square Nail (833 mm); both lowest and highest evapotranspiration were at Weber Creek (387 to 476 mm), likely as a result of the varied aspect (N to W) at this site.

Soils were not highly variable; all but two locales had the most common soil type on the Pine Hill formation, RgE2 (Rescue extremely stony sandy loam, 3 to 50 percent slopes, eroded); locale 2343 had RfC (Rescue very stony sandy loam, 3 to 15 percent slopes), and locale 2345 had RfE (Rescue very stony sandy loam, 30 to 50 percent slopes).

Most of the sampled locales have never experienced wild or controlled fire, at least since records began to be maintained by the state of California in the late 19th century (Table 1). The only two exceptions are Ponderosa (locale 2343), which

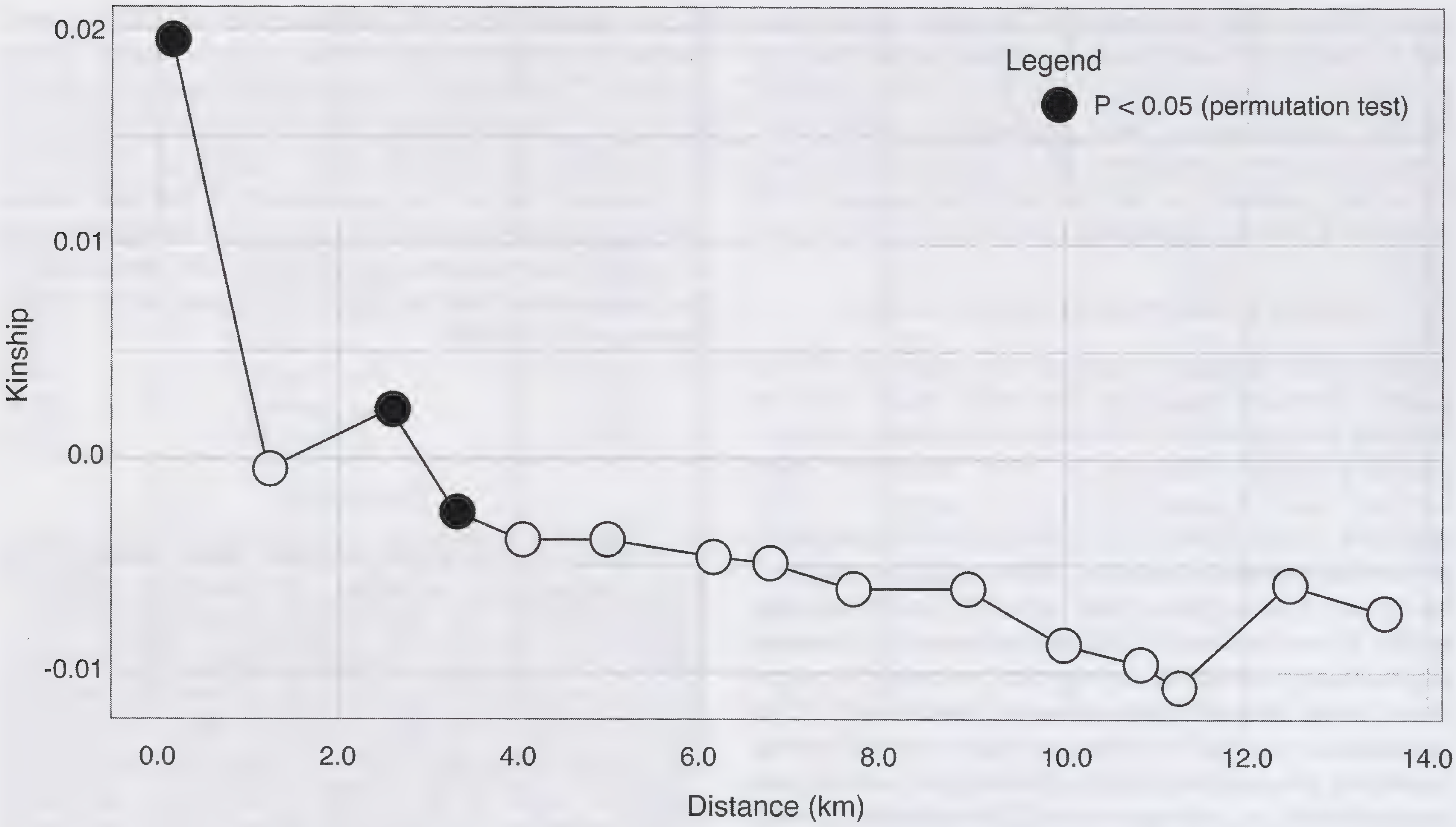

FIG. 2. Spatial autocorrelation. Results of spatial autocorrelation analysis with the *eco.malecot* algorithm of the R package *EcoGenetics* (method = global, nclass = 3). Distance is great circle distance; kinship is Nason's F_{ij} (Loiselle et al. 1995).

experienced a fire in 2007, and Weber Creek (locale 2344), with a fire in 1964. Although fires have burned in the vicinity of some of the other locales, potentially affecting nearby populations of the focal species, these fires did not burn the habitat occupied by the plants that were sampled in these areas.

Population Genetics

Allelic diversity varied from 7093 (locale 2345) to 7475 (locale 2347; Table 2). Expected heterozygosity varied from 0.019 (locales 2342, 2344, and 2345) to 0.022 (locales 2341 and 2347). Genetic differentiation (F_{st}) varied from 0.02 (locale 2340 versus 2347) to 0.04 (locale 2343 versus 2344). Results of F_{st} analysis are at the Dryad Digital Repository (Appendix S5, doi.org/10.5061/dryad.n02v6wwt2). The result of Goudet's G-statistic Monte Carlo test was significant (P = 0.001; observation: 1189.7; standard deviation of observation: 7.8 ; expectation: 992.7; variance: 643.2), suggesting that there is significant hierarchical structuring of the locales. For tests of isolation by distance, the Spearman method yielded a significant result (P = 0.03; Mantel r statistic: 0.06), while the Pearson method did not (P = 0.08; Mantel r statistic: 0.05). Spatial autocorrelation was detected by *EcoGenetics* in only three of the lowest distance categories: 1) 0-890 m, 2) 890-1890 m, and 3) 2770-3770 m (permutation test: $P < 0.05$; Fig. 2).

Results of the Evanno method (Evanno et al. 2005) applied to STRUCTURE output imply that three ancestral groups is most optimal. A summary of the Evanno et al. (2005) method applied to the STRUCTURE output is at Dryad Digital Repository (Appendix S6, doi.org/10.5061/dryad.n02v6wwt2). The STRUCTURE plot for K = 3 (Fig. 3) shows that locales 2343 and 2345 are the most distinct, as they are dominated by two ancestral groups (Ancestral Groups 2 and 3) that are represented in other locales, but are not common. The remaining locales are dominated by Ancestral Group 1.

Redundancy Analysis

RDA on environmental versus genetic data, controlling for latitude and longitude, yielded a significant overall model (F = 2.09, df = 3, P = 0.01), but only the first axis was significant on its own (RDA1: F = 3.63, df = 1, P = 0.01; RDA2: F = 1.53, df = 1, P = 0.09; RDA3: F = 1.12, df = 1, P = 0.25). Out of the three climatic variables tested, only elevation was significant (elev: F = 1.42, df = 1, *P* = 0.04; cwd: F = 1.30, df = 1, *P* = 0.07; aet: F = 1.30, df = 1, *P* = 0.09). A plot of the first two axes (Appendix S7, doi.org/10.5061/dryad.n02v6wwt2) shows the association of climate with genetics, the primary differentiation occurring between the lower-elevation locales (2340, 2345, and 2347) and the higher elevation locales (2341-2344); the higher elevations locales are all in the vicinity of Pine Hill (Fig. 1).

DISCUSSION

Clonality

The first ecological research on *W. reticulata* suggested that under natural conditions, the species

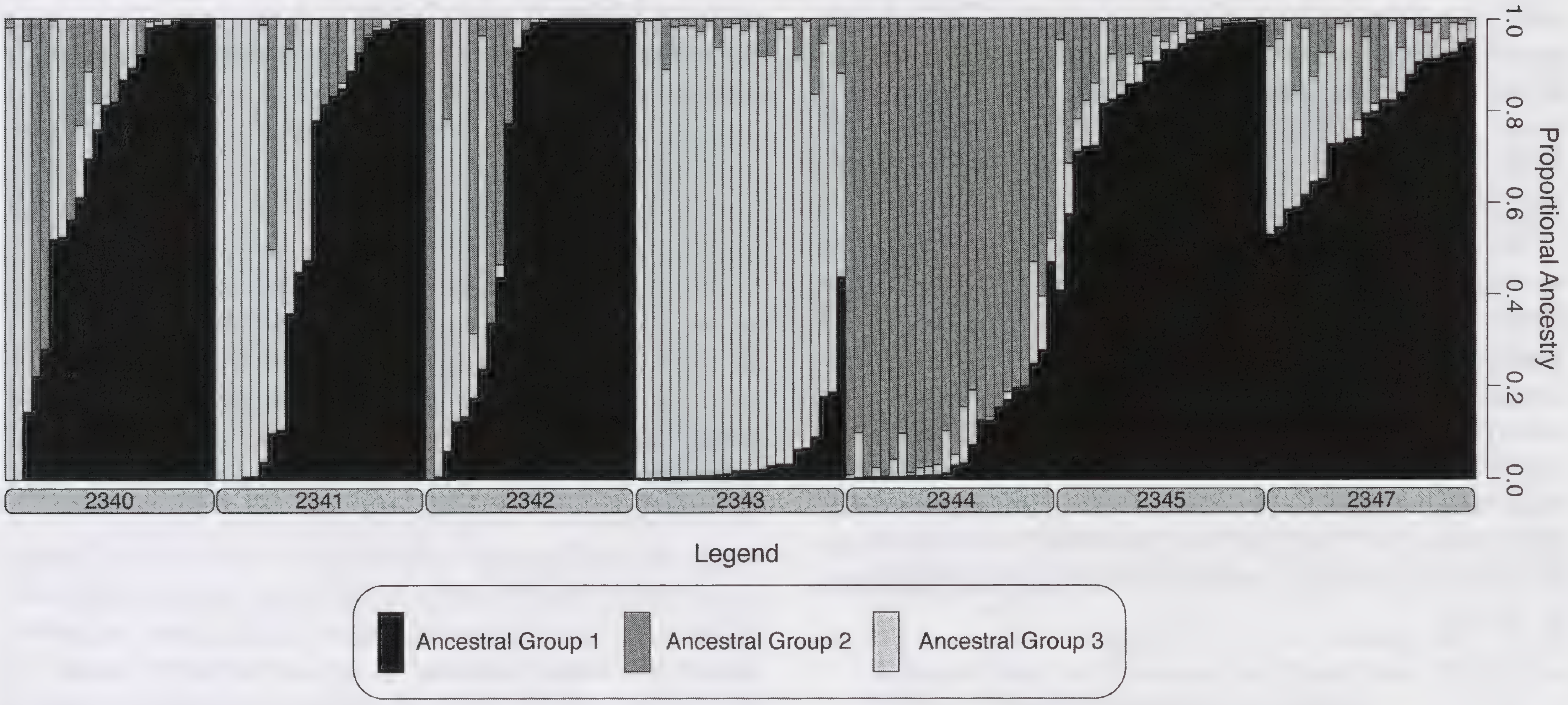

FIG. 3. Proportional genetic ancestry based on analysis of genotypic data in STRUCTURE. Results of analysis with the program STRUCTURE, assuming three ancestral groups (see Materials and Methods). Under the assumption that three ancestral groups are present, STRUCTURE estimated that proportion of genetic variation in each sampled individual that was assignable to each of these groups. Proportions are indicated by shaded columns, and are the average across all 10 of the runs for K = 3.

reproduced sexually almost exclusively in the aftermath of wildfire (Ayers 1997), and that in intervening periods, reproduction was likely asexual, via an underground rhizome that allows the plant to spread over large areas of habitat (Ayers 1997). Molecular genetic research (Ayers and Ryan 1997, 1999) supported this idea, finding that diversity was low within populations, but higher amongst populations. These results are in contrast to the results presented here, in which less than 2% of the 168 stems were identified as being derived from asexual reproduction. These results suggest either that 1) clones are only present at a very fine spatial scale (less than the 5.6 m minimum distance amongst sampled plants used in this study—see Materials and Methods) or that 2) clonal reproduction is not as common in this species as previously assumed. It may also be possible that some of the MLGs do represent ramets descended from one genet by asexual reproduction, but with sufficient somatic mutations after separation from the parent plant that the ramets appear to be separate genets. Although the methods used should account for such somatic mutations, these methods also assume a relatively low level of such change, while the potentially long-lived stands thought to occur in this species (Ayers 1997) could result in the accumulation of a large number of somatic mutations over the course of many years.

Population Differentiation

The sampled locales represent all of the major population centers of the species, and the complete range of environmental conditions under which the plant occurs. The results presented here suggest that there is population differentiation (Fig. 3) that is not entirely due to isolation by distance. Most significantly, there are two genetically distinct locales (2343 and 2344) that are dominated by separate ancestral genetic groups; these locales are located at opposite ends of the geographic range of the species (Fig. 1), suggesting isolation by distance. On the other hand, the Square Nail locale (2342), located less than one km from the Weber Creek locale (2344), is not closely allied to plants at this locale. One potential explanation of this pattern is that the dispersal barrier posed by the American River Canyon has resulted in differentiation of these locales. A similar situation is found at the southern end of the species' range, where the Ponderosa locale (2343, Fig. 1) is dominated by a different ancestral group than the nearby Cameron Park locale (2341), despite the close proximity of the locations. Overall, a single ancestral group, Ancestral Group 1 (Fig. 3), dominates the core of the species' range, centered on the higher elevation terrain that surrounds Pine Hill (Fig. 1). However, the genetic signature of the other two ancestral groups is significant in all of the other sampled locales, suggesting that genetic exchange among locales is more likely to take place out of, rather than into, the two isolated peripheral populations (2343 and 2344) where the signature of these ancestral genetic groups is most common (Fig. 3).

Ecological Correlates of Genetic Patterns

Redundancy analysis (RDA) revealed that only elevation was significantly associated with genetics. In the RDA plot (Appendix S7, doi.org/10.5061/dryad.n02v6wwt2), three of the highest elevation locales (2340, 2345, and 2347) are strongly differentiated from three lower elevation locales (2342-44), with one intermediate elevation locale (2341) bridging the gap. The results seem to support the findings of the clustering analysis (Fig. 3) in which locales from Pine Hill and its associated uplands (2340, 2345, 2347; Fig. 1) are dominated by a single Ancestral Group, Ancestral Group 1. However, this same group is also at a high frequency in two other locales that are at lower elevations, outside the immediate vicinity of Pine Hill (2341 and 2342). These results seem to suggest that the divergent climate of Pine Hill and its associated uplands may have played a role in population differentiation in *W. reticulata*, and may continue to do so in the future. This may constitute a form of intraspecific local adaptation, of the kind that has been found to occur in the closely related sunflowers, *Helianthus* (Baack et al. 2015).

Conservation Implications

Management and conservation of rare plants demands knowledge of population genetic patterns (Allendorf et al. 2010). Data of this kind can be used to 1) prioritize acquisition of lands that support unique genetic subunits of the species (Petit et al. 1998; Diniz-Filho et al. 2012), 2) set stringency of protection measures for populations depending on their genetic distinctiveness (Petit et al. 1998; Diniz-Filho et al. 2012), and 3) select germplasm for ex-situ conservation and re-population programs (Guerrant et al. 2014; Hoban and Schlarbaum 2014; Mijangos et al. 2015). Data presented here suggest that future land acquisition to support conservation of *W. reticulata* should probably prioritize populations at the periphery, especially at the southern and northern ends of the Pine Hill formation (Fig. 1), as these are the areas where the most genetically isolated plants are found (Fig. 3). These locations are also where populations on lands that are already under conservation should be more carefully conserved (Petit et al. 1998). Finally, these same populations should be a priority for seed-banking (Guerrant et al. 2014; Hoban and Schlarbaum 2014; Mijangos et al. 2015).

As discussed above, data presented here also suggest that clonality may not be as common in *W. reticulata* as once thought, though some populations show the genetic signature of this mode of reproduction (Table 2). This has clear conservation implications, as the amount of clonal reproduction taking place determines the genetic variability of the populations, which in turn influences the speed at which populations adapt; highly clonal populations and species may not contain sufficient genetic variation to respond effectively to environmental changes such as habitat fragmentation, climatic shifts, and arrival of invasive species or pathogens (Loehle 1987; Eckert 2002). While genetic diversity is low in *W. reticulata*, the data do not support a high rate of asexual reproduction, at least at the scale that the stems were surveyed (greater than 5.6 m horizontal distance). However, some locales, most notably Weber Creek (2344) and Farview (2345; Fig. 1) do show a relatively strong genetic signature of clonal reproduction, as measured by the index of association (Table 2). It is not clear why these populations are more clonal than others; further research should be carried out to determine the conditions that predict clonality.

Additional research is clearly needed on the population genetics and ecology of this rare species. In particular, additional data on the reproductive ecology of the species is needed. As past research has shown that sexual reproduction is strongly associated with fire and other kinds of major disturbance (e.g., bulldozing), and thus highly episodic (Ayres 1997), it is not clear why clonal reproduction has yet not come to completely dominate population genetic patterns in the species. Fine-scale population genetics (below 5.6 m horizontal distance) on continuous stands of the species would help to unravel the scale at which clonality might occur. It would be especially interesting to excavate underground rhizomes to confirm which stems are ramets, and to compare the genetic profiles of these stems to the seeds that they produce, as this would help to place a threshold on the expected amount of genetic divergence among stems derived from asexual versus sexual reproduction (Arnaud-Haond et al. 2007a). More experiments on demographic response to fire and other disturbance should also be carried out, as the results of such research would lead to the development of management tools, for example disturbance to promote sexual reproduction, that could be used to maintain genetic diversity in this rare species.

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LITERATURE CITED

AGAPOW, P.-M. AND A. BURT. 2001. Indices of multilocus linkage disequilibrium. Molecular Ecology Resources 1:101–102.

ALLENDORF, F. W., P. A. HOHENLOHE AND G. LUIKART. 2010. Genomics and the future of conservation genetics. Nature Reviews Genetics 11:697–709.

ARNAUD-HAOND, S. AND K. BELKHIR. 2007. GENCLONE: a computer program to analyse genotypic data, test for clonality and describe spatial clonal organization. Molecular Ecology Notes 7:15–17.

ARNAUD-HAOND, S., C. M. DUARTE, F. ALBERTO, AND E. A. SERRÃO. 2007. Standardizing methods to address clonality in population studies. Molecular Ecology 16:5115–5139.

ARONESTY, E. 2013. Comparison of sequencing utility programs. The Open Bioinformatics Journal 7:1–8.

AYRES, D. R. 1997. The clonal and population biology of *Wyethia reticulata* (Asteraceae), a rare perennial of the chaparral. Unpublished Ph.D. dissertation, University of California, Davis, CA.

AYRES, D. R., AND F. J. RYAN. 1997. The clonal and population structure of a rare endemic plant, *Wyethia reticulata* (Asteraceae): allozyme and RAPD analysis. Molecular Ecology 6:761–772.

AYRES, D. R., AND F. J. RYAN. 1999. Genetic diversity and structure of the narrow endemic *Wyethia reticulata* and its congener *W. bolanderi* (Asteraceae) using RAPD and allozyme techniques. American Journal of Botany 86:344–353.

BAACK, E., M. C. MELO, L. H. RIESEBERG, AND D. ORTIZ-BARRIENTOS. 2015. The origins of reproductive isolation in plants. New Phytologist 207:968–984.

BAILLEUL, D. S. STOECKEL, AND S. ARNAUD-HAOND. 2016. RClone: a package to identify Multilocus Clonal Lineages and handle clonal datasets in R. Methods in Ecology and Evolution 7:966–970.

BOURRET, V., M. DIONNE, L. BERNATCHEZ. 2014. Detecting genotypic changes associated with selective mortality at sea in Atlantic salmon: polygenic multilocus analysis surpasses genome scan. Molecular Ecology 23:4444–4457.

CALIFORNIA DEPARTMENT OF FORESTRY ND FIRE PROTECTION'S FIRE AND RESOURCE ASSESSMENT PROGRAM (FRAP). 2019. CAL FIRE Resource Assessment Program Fire Perimeters. Website: https://frap.fire.ca.gov/ [accessed DD Month YYYY].

CALIFORNIA NATIVE PLANT SOCIETY (CNPS). 2019. Inventory of Rare and Endangered Plants of California (online edition, v8-03 0.39). CNPS Rare Plants Program, Sacramento, CA. Website: http://www.rareplants.cnps.org [accessed 24 May 2019).

CLARK, L. V. AND M. JASIENIUK. 2011. Polysat: an R package for polyploid microsatellite analysis. Molecular Ecology Resources 11:562–566.

DANECEK, P., A. AUTON, G. ABECASIS, C. A. ALBERS, E. BANKS, M. A. DEPRISTO, R. E. HANDSAKER, G. LUNTER, G. T. MARTH, S. T. SHERRY, G. MCVEAN, R. DURBIN, AND THE 1000 GENOME PROJECT ANALYSIS GROUP. 2011. The variant call format and VCFtools. Bioinformatics 27:2156–2158.

DAVEY, J. W., T. CEZARD, P. FUENTES-UTRILLA, C. ELAND, K. GHARBI, AND M. L. BLAXTER. 2013. Special features of RAD Sequencing data: implications for genotyping. Molecular Ecology 22:3151–3164.

DINIZ-FILHO, J. A. F., D. B. MELO, G. DE OLIVEIRA, R. G. COLLEVATTI, T. N. SOARES, J. C. NABOUT, J. S. DE LIMA, ET AL. 2012. Planning for optimal conservation of geographical genetic variability within species. Conservation Genetics 13:1085–1093.

DIXON, P. 2003. VEGAN, a package of R functions for community ecology. Journal of Vegetation Science 14: 927–930.

DOUHOVNIKOFF, V. AND R. S. DODD. 2003. Intra-clonal variation and a similarity threshold for identification of clones: application to *Salix exigua* using AFLP molecular markers. Theoretical and Applied Genetics 106:1307–1315.

EARL, D. A., AND B. M. VONHOLDT. 2012. STRUCTURE HARVESTER: a website and program for visualizing STRUCTURE output and implementing the Evanno method. Conservation Genetics Resources 4:359–361.

ECKERT, C. G. 2002. The loss of sex in clonal plants. Evolutionary Ecology 15:501–520.

EVANNO, G., S. REGNAUT, AND J. GOUDET. 2005. Detecting the number of clusters of individuals using the software STRUCTURE: A simulation study. Molecular Ecology 14:2611–2620.

FALUSH, D., M. STEPHENS, AND J. K. PRITCHARD. 2003. Inference of population structure using multilocus genotype data: linked loci and correlated allele frequencies. Genetics 164:1567–1587.

FALUSH, D., M. STEPHENS, AND J. K. PRITCHARD. 2007. Inference of sampling locale structure using multilocus genotype data: Dominant markers and null alleles. Molecular Ecology Notes 7:574–578.

FLINT, L. E., A. L. FLINT, J. H. THORNE, AND R. BOYNTON. 2013. Fine-scale hydrologic modeling for regional landscape applications: the California Basin Characterization Model development and performance. Ecological Processes 2:25.

FORESTER, B. R., J. R. LASKY, H. H. WAGNER, AND D. L. URBAN. 2018. Comparing methods for detecting multilocus adaptation with multivariate genotype-environment associations. Molecular Ecology 27:2215–2233.

GOUDET, J. 2005. HIERFSTAT, a package for R to compute and test hierarchical F-statistics. Molecular Ecology Notes 5:184–186.

GOUDET, J., AND T. JOMBART. 2015. hierfstat: Estimation and tests of hierarchical F-statistics. R package version 0.04-22. http://CRAN.R-project.org/package=hierfstat

GUERRANT, E. O., K. HAVENS, AND P. VITT. 2014. Sampling for effective ex situ plant conservation. International Journal of Plant Sciences 175:11–20.

HARPER, J. L. 1977. Population biology of plants. Academic Press, London.

HIJMANS, R. J. 2017. raster: geographic data analysis and modeling. R package version 2.6-7. http://CRAN.R-project.org/package=raster

HIPP, A. L., D. A. R. EATON, J. CAVENDER-BARES, E. FITZEK, R. NIPPER, AND P. S. MANOS. 2014. A framework phylogeny of the American oak clade based on sequenced RAD data. PLOS ONE 9:e102272.

HOBAN, S., AND S. SCHLARBAUM. 2014. Optimal sampling of seeds from plant populations for ex-situ conservation of genetic biodiversity, considering realistic population structure. Biological Conservation: 77:90–99.

HUBISZ, M. J., D. FALUSH, M. STEPHENS, AND J. K. PRITCHARD. 2009. Inferring weak population structure with the assistance of sample group information. Molecular Ecology Resources 9:1322–1332.

HUNTER, J. C. AND J. E. HORENSTEIN. 1991. The vegetation of the Pine Hill area (California) and its relation to substratum. Pp. 197-206 *in* A. J. M. Baker, J. Proctor, and R. D. Reeves (eds.), The vegetation of ultramafic (serpentine) soils. Intercept, Andover, United Kingdom.

JOMBART, T. 2008. Adegenet: a R package for the multivariate analysis of genetic markers. Bioinformatics 24:1403–1405.

JOMBART, T. AND I. AHMED. 2011. Adegenet 1.3-1: new tools for the analysis of genome-wide SNP data. Bioinformatics 27:3070–3071.

KAMVAR, Z. N., J. F. TABIMA, AND N. J. GRÜNWALD. 2014. Poppr: an R package for genetic analysis of populations with clonal, partially clonal, and/or sexual reproduction. PeerJ 2:e281.

KAMVAR, Z. N., J. C. BROOKS, AND N. J GRÜNWALD. 2015. Novel R tools for analysis of genome-wide population genetic data with emphasis on clonality. Frontiers in Genetics 6:208.

KEIL, D. J. 2012. *Wyethia.* Pages ##-## *in* B. G. Baldwin et al. (eds.), The Jepson manual: vascular plants of

California. University of California Press, Berkeley, CA.

Langmead, B., C. Trapnell, M. Pop, and S. L. Salzberg. 2009. Ultrafast and memory-efficient alignment of short DNA sequences to the human genome. Genome Biology 10:R25.

Li, H. and R. Durbin. 2009. Fast and accurate short read alignment with Burrows–Wheeler transform. Bioinformatics 25 14:1754–1760.

Li, H., B. Handsaker, A. Wysoker, T. Fennell, J. Ruan, N. Homer, G. Marth, G. Abecasis, R. Durbin, and the 1000 Genome Project Data Processing Subgroup. 2009. The sequence alignment/map format and SAMtools. Bioinformatics 25:2078–2079.

Loehle, C. 1987. Partitioning of reproductive effort in clonal plants: a benefit-cost model. Oikos, 49:199–208.

Loiselle, B., V. Sork, J. Nason, and C. Graham. 1995. Spatial genetic structure of a tropical understory shrub, *Psychotria officinalis* (Rubiaceae). American Journal of Botany 82:1420–1425.

Lozier, J. D. 2014. Revisiting comparisons of genetic diversity in stable and declining species: assessing genome-wide polymorphism in North American bumble bees using RAD sequencing. Molecular Ecology 23:788–801.

Mardis, E. R. 2017. DNA sequencing technologies: 2006–2016. Nature Protocols 12:213–218.

Meirmans, P. G., and P. H. Van Tienderen. 2004. GENOTYPE and GENODIVE: two programs for the analysis of genetic diversity of asexual organisms. Molecular Ecology Notes 4:792–794.

Mijangos, J. L, C. Pacioni, P. B. S. Spencer, and M. D. Craig. 2015. Contribution of genetics to ecological restoration. Molecular Ecology 24:22–37.

Moore, A. J. and L. Bohs. 2003. An ITS phylogeny of *Balsamorhiza* and *Wyethia* (Asteraceae; Heliantheae). American Journal of Botany 90:1653–1660.

Nei, M. 1978. Estimation of average heterozygosity and genetic distance from a small number of individuals. Genetics 89:583–90.

Oksanen, J., F. G. Blanchet, R. Kindt, P. Legendre, P. R. Minchin, R. B. O'Hara, G. L. Simpson, P. Solymos, M. H. Stevens, and H. Wagner. 2018. vegan: community ecology package. R package version 2.5-1. Website: http://CRAN.R-project.org/package=vegan [accessed DD Month YYYY].

Petit, R. J., E. A. Mousadik, and O. Pons. 1998. Identifying populations for conservation on the basis of genetic markers. Conservation Biology 12:844–855.

Pritchard, J. K., M. Stephens, and P. Donnelly. 2000. Inference of sampling locale STRUCTURE using multilocus genotype data. Genetics 155:945–959.

Schlarbaum, H. S. 2014. Optimal sampling of seeds from plant populations for ex-situ conservation of genetic biodiversity, considering realistic population structure. Biological Conservation 177: 90–99.

Smith, J. M., N. H. Smith, M. O'Rourke, and B. G. Spratt. 1993. How clonal are bacteria? Proceedings of the National Academy of Sciences 90:4384–4388.

United States Department of Agriculture (USDA). 2019. Web soil survey. Natural Resources Conservation Service. Website: https://www.nrcs.usda.gov/wps/portal/nrcs/main/soils/survey/ [accessed 1 June 2019].

United States Fish and Wildlife Service (USFWS). 2002. Recovery plant for gabbro soil plants of the Central Sierra Nevada foothills. USFWS, Portland, OR.

Wilson, J. L. 1986. A study of plant species diversity and vegetation patterns associated with the Pine Hill gabbro formation and adjacent substrata, El Dorado County, California. Unpublished M.S. thesis. California State University, Sacramento, CA.

Wilson, J. L., D. R. Ayres, S. Steinmaus, and M. Baad. 2009. Vegetation and flora of a biodiversity hotspot: Pine Hill, El Dorado County, California, USA. Madroño 56:246–278.

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VARIATION IN LEAF SHAPE IN A *QUERCUS LOBATA* COMMON GARDEN: TESTS FOR ADAPTATION TO CLIMATE AND PHYSIOLOGICAL CONSEQUENCES

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ABSTRACT

Oak leaf morphology is highly variable. Leaf shape in oaks has been shown to covary with climate, and leaf dissection is negatively correlated with hydraulic resistance. Such patterns may reflect local adaptation of genotypes or plastic responses to local environments. We tested two hypotheses regarding variation in leaf shape in *Quercus lobata* Née, a widely distributed oak tree endemic to California, using subsamples of trees from a large provenance trial involving source populations throughout the species range. First, we tested the hypothesis that variation in leaf dissection (perimeter · area^{-1}) and specific leaf area could be explained by adaptation to climate. If so, we predicted that the progeny of trees originating from contrasting climates would also contrast in leaf dissection or specific leaf area when grown in a common environment. Second, we tested the hypothesis that variation in leaf dissection is associated with photosynthetic rate. Because dissection affects hydraulic resistance and heat transfer, more dissected leaves are thought to experience lower water stress. If so, we predicted that individuals with more dissected leaves would maintain higher rates of photosynthesis than those with less dissected leaves, especially during hot and dry conditions. We found no association of leaf traits with maternal climate, but we observed a positive relationship between leaf dissection and photosynthetic rates. This result suggests variation in leaf shape may have functional consequences and influence how valley oaks cope with environmental stress in California's Mediterranean climate.

Key Words: adaptation, climate, common garden, dissection, leaf shape, photosynthesis, *Quercus lobata*, water stress.

Leaves are the primary organs of carbon assimilation, water relations, and energy balance in plants, and thus leaf traits that affect fitness, such as morphology, may be under strong selection, with optimal leaf morphology depending on local environmental conditions (Givnish 1978; Wright et al. 2005; Ferris 2019). The shape of leaves can affect plant thermoregulation, vulnerability to drought, resistance to herbivory, and light interception, among other processes (Nicotra et al. 2011; Ferris 2019), any of which may have consequences for plant survival and reproduction. The potential for local adaptation in leaf traits should be especially pronounced in widely distributed species that experience substantial variation in local climatic conditions (Valladares et al. 2000; Royer 2012; Ramírez-Valiente et al. 2017a).

Oaks (genus *Quercus*) are well known for harboring substantial intraspecific variation in leaf morphology, and this variation may reflect different ecological strategies (Jensen 1990; Valladares et al. 2000). Previous studies, for example, have shown that specific leaf area and leaf shape of some oak species covary with climatic variables, including temperature and precipitation (Kolb et al. 1990; Valladares et al. 2000; MacDonald 2017) and elevation (Albarrán-Lara et al. 2015). Ramírez-Valiente et al. (2017b), for example, reported that genetically based variation in functional leaf traits among populations of *Q. oleoides* Schltdl. & Cham., including specific leaf area and lamina size, resulted from adaptation to precipitation regimes. In addition, Sisó et al. (2001) found that leaf dissection is negatively associated with hydraulic resistance in several North American *Quercus* species, indicating a functional consequence of leaf dissection that may drive adaptation. Leaf dissection appears to improve heat transfer (Gurevitch and Schuepp 1990), which likely is adaptive for plants exposed to high temperatures. Taken together, studies of oaks suggest that leaf morphological variation adaptively mediates responses to the environment (e.g., Abrams 1990; Cavender-Bares et al. 2004; Riordan et al. 2016).

In this study, we tested two hypotheses regarding variation in leaf morphology of *Quercus lobata* Née, California's valley oak, in the context of a large common garden experiment (Delfino-Mix et al.

2015). Leaf morphology in valley oak has been found to vary with elevation (Albarrán-Lara et al. 2015) and to differ genetically among populations (MacDonald 2017). In addition, the broad topographic and geographic distribution of valley oak, including the Central Valley, Sierra Nevada foothills, and Costal Ranges of California (Tyler et al. 2006) suggests that the substantial variation in climate across its range may have imposed selection on important morphological and physiological traits (MacDonald 2017; Browne et al. 2019). First, we tested the idea that variation in leaf morphology is explained by adaptation to the climate in which a population evolves. If so, we predicted that trees grown from acorns originating in contrasting climates would differ in leaf morphology even when grown in a common garden. Second, we tested the hypothesis that variation in leaf morphology is associated with photosynthetic rate. Higher photosynthetic rates are positively associated with individual fecundity (e.g., Arntz et al. 2000) and population growth (e.g., Westerband and Horvitz 2017) in many plants (reviewed in Ackerley et al. 2000). Sisó et al. (2001) found that more dissected leaves of several *Quercus* species experienced reduced hydraulic resistance, which may allow individuals with dissected leaves to have improved water balance, especially during periods of drought stress. If leaf dissection ameliorates water stress, we predict that more dissected leaves would have higher carbon assimilation rates (a measure of photosynthesis), particularly during periods of water stress, given the demands of photosynthesis for water use.

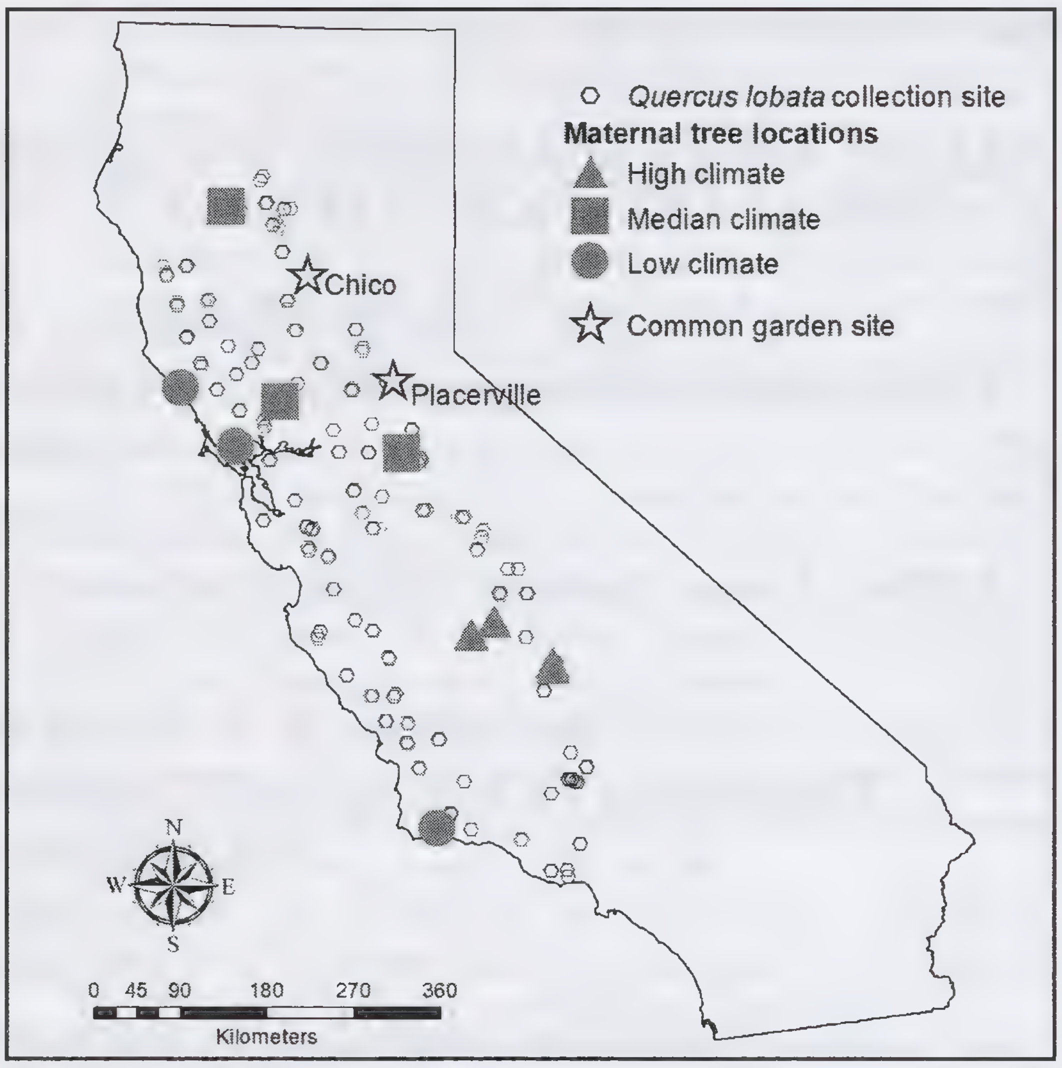

FIG. 1. Map of California showing the localities from which *Quercus lobata* acorns were collected (open hexagons) to establish the two provenance trials (open stars) in Chico and Placerville. Localities of family lines subsampled from high (triangle), median (square), and low (circle) climate categories indicated with shaded symbols (see Methods).

METHODS

Study Species

Valley oak (*Quercus lobata* [Fagaceae]) is an iconic, keystone species within California, and it provides a useful study system because of its broad geographic range, as well as the availability of extensive background information. Valley oak populations harbor fine-scale genetic structure (Dutech et al. 2005), leading to the potential for local adaptation to environmental conditions. This structure is likely a consequence of relatively restricted effective distances of pollen-mediated and seed-mediated gene flow (Sork et al. 2002; Grivet et al. 2005; Grivet et al. 2009; Sork et al. 2015). In addition, genetic structure for putatively neutral loci (Sork et al. 2010; Gugger et al. 2013), as well as non-neutral loci (Sork et al. 2016) has been shown to be correlated with climate gradients, which supports the idea that this species has adapted to climate (see also Browne et al. 2019). Moreover, valley oak leaves appear to harbor substantial morphological variation, from genetic as well as environmental sources (MacDonald 2017). A range-wide field study of valley oaks reported geographic variation in morphological as well as physiological traits (R. Coria, K. D. Gaddis, J. M. Espelta, and V. L. Sork, unpublished data). Valley oak is currently threatened throughout its range (Tyler et al. 2006; Mclaughlin and Zavaleta 2012) due to extensive habitat loss (Whipple et al. 2011), and the species is predicted to experience a substantial reduction in available habitat within the next century due to climate change (Kueppers et al. 2005; Sork et al. 2010). In addition, valley oak is sensitive to water stress, especially as seedlings (Meyer 2002).

Experimental Design

This study was conducted using a large fully replicated provenance test established at two locations, in which acorns collected from maternal trees were grown in a common environment (for details of study see Delfino-Mix et al. 2015). In fall 2012, 20 acorns were collected from each of 672 mature trees at 95 localities (provenances) across the native range of valley oak. On 14 and 15 November 2012, up to 16 surface-sterilized acorns within a maternal family (total 10,326) were planted into containers and reared in a lath house under 50% shade cover. In late 2014 and early 2015, five saplings (maternal families) from each sampled mature tree were transplanted into large field plots using a randomized block design at each of two locations: (1) the Chico Seed Orchard ("Chico") in Chico, CA and (2) the Institute of Forest Genetics ("Placerville") in Placerville, CA (Fig. 1). The two sites are quite distinct climatically, but both fall within the range of climate variation across the sites from which acorns were collected (Delfino-Mix et al. 2015). Chico is a warmer, drier climate (68 m elevation; Mean Annual Temperature [MAT] 16.4 °C; Mean Annual Precipitation [MAP] 64.1cm), while Placerville has a cooler, wetter climate (838 m elevation; MAT 14.5°C; MAP 103.8cm; Wang et al. 2016). Both tests were irrigated periodically during summers during our study, and competing vegetation was controlled with mowing and herbicide. See Delfino-Mix et al. (2015) for more information about sampling, cultivation, and design of the provenance trial.

Sampling and traits

To test for leaf morphological adaptation to climate, we identified a subset of 180 trees within the provenance test representing the extremes and median of multivariate maternal climatic conditions based on a principal component analysis of a 30-year (1971-2000) georeferenced baseline dataset of 23 annual climate variables (Wang et al. 2016) at the source locations for the 672 maternal lineages. Six maternal lines were selected from among each of the highest, lowest, and median scores for the first principal component of all climate variables with the stipulation that no more than two maternal lines were selected from one locality (Fig. 1). The first principal component explained 43.8% of the variance in the climate data and was most strongly associated with variables involving temperature and seasonality (strongest positive factor loadings included mean annual temperature [0.28], degree-days > 5°C [0.28], and number of frost-free days [0.25]; strongest negative factor loadings included degree-days below 18°C [-0.30], mm precipitation as snow [-0.27], and degree-days below 0°C [-0.25]). We haphazardly sampled five leaves from all progeny ($n = 5$) from each of the 18 focal maternal lineages within each of the two experimental sites (Chico and Placerville; because progeny mortality led to incomplete sampling, the total trees sampled = 141 and total leaves sampled = 707). We measured the area (mm^2) and perimeter (mm) of each leaf from scanned images of fresh leaves using ImageJ (Schneider et al. 2012). Leaves were then dried to constant mass at 50°C, and dry biomass of each leaf was recorded to the nearest mg using an analytical balance. Measurements were used to calculate specific leaf area (area · dry $biomass^{-1}$ in $mm^2 \cdot g^{-1}$) and leaf dissection (perimeter · $area^{-1}$ in $mm \cdot mm^{-2}$).

To test the association between leaf morphology and photosynthesis, we selected trees to subsample within the Chico site using leaf trait data collected by MacDonald (2017), which included all progeny from all 672 maternal lines within both experimental sites. MacDonald's (2017) study tested the effects of maternal climate on plasticity (or variation) in leaf traits, whereas the current study examined mean differences in traits among climate extremes as described by the PCA scores (see above). During 2016, MacDonald (2017) measured morphological traits on five leaves from each of the 3360 trees within each of the two common garden locations. Using this larger dataset, we selected 24 of the 672 maternal lines within Chico that had mean values of leaf dissection that were high (mean [SD] = 3.553 [0.157]), intermediate (2.628 [0.003]), or low (2.038 [0.056]) as reported by MacDonald (2017). Our objective with this approach was to sample trees representing a broad range of leaf dissection values across the experiment. By focusing on these lines, we assumed – and were able to test (see Results) – that variation in leaf morphology between years within a maternal line would be smaller than variation among lines.

Using a portable infra-red gas analyzer (Li-Cor 6400, LI-COR Biosciences, Lincoln, NE) we measured carbon assimilation (A, $\mu mol\ CO_2 \cdot m^{-2} \cdot s^{-1}$) on three leaves from each of a total of 28 progeny chosen among 17 of the 24 targeted maternal lines to maximize representation across expected leaf dissection values, based on measurements from 2016 (MacDonald 2017). Time constraints required for measurements with the instrument (e.g., internal equilibration required about 15 min for each leaf before measurements could be recorded) limited the number of trees we were able to sample. Measurements were collected across six days in 2018 (18, 19, 26, 29 June and 9, 13 July) in the morning between 0800 and 1200 h, prior to midday stomatal closure when photosynthetic rates fell to zero. The site was irrigated once during this period on 22 June 2018. Leaves were selected based on appearance (no apparent damage from herbivores). Internal chamber settings were as follows: photosynthetically active radiation (PAR) = 1500 $\mu mol \cdot s^{-1}$; stomatal ratio = 1.0; flow = 500 $\mu mol \cdot s^{-1}$; and reference chamber CO_2 concentration = 400 ppm. For leaves that were too small or deeply lobed to completely fill the area of the 2 cm^2 chamber, the area of leaf tissue inside the chamber was calculated manually by tracing the edges of the leaf inside the chamber with ink, removing the leaf from the tree, and later scanning an image of the leaf using a digital scanner. We then used ImageJ (Schneider et al. 2012) to estimate the measured area of each leaf, and gas exchange estimates were adjusted based on these values using the Li-Cor recompute utility. In addition, we used ImageJ to measure the area (mm^2) and perimeter (mm) of each leaf, which were then used to calculate leaf dissection as described above.

Analysis

Analyses were conducted using SAS version 9.3 (SAS Institute, Cary, NC). Specific leaf area and leaf dissection were each compared across climate categories (high, median, low) using mixed-model nested ANOVAs with the Kenward-Roger approximation for degrees of freedom. Climate category and locality(category) were included as fixed effects, and maternal family (category x locality) and individual tree (category x locality x family) were included as

TABLE 1. MIXED-MODEL ANALYSES OF VARIANCE OF SPECIFIC LEAF AREA ($\text{MM}^2 \cdot \text{G}^{-1}$) AND LEAF DISSECTION ($\text{MM} \cdot \text{MM}^{-2}$) AMONG *QUERCUS LOBATA* LEAVES SAMPLED FROM 180 SAPLINGS (10 PROGENY FROM EACH OF 18 FAMILIES, ORIGINATING FROM 9 LOCALITIES) PLANTED IN TWO COMMON GARDENS. Sampled trees were selected to represent extremes and median of multivariate climatic conditions of maternal source trees (see Methods). F-tests of fixed effects and χ^2 values from likelihood-ratio tests of random effects are shown.

Test site	Trait	Effect type	Source	$F_{\text{ndf,ddf}}$ or χ^2	*P*-value
Chico	Specific leaf area	Fixed	Maternal climate category	$0.61_{2,\ 65}$	0.5
			Locality (category)	$1.14_{6,65}$	0.3
		Random	Family (category x locality)	0.0	0.9
			Individual tree (category x locality x family)	163.9	<0.0001
	Leaf dissection	Fixed	Maternal climate category	$0.02_{2,\ 65}$	0.9
			Locality (category)	$1.41_{6,\ 65.1}$	0.2
		Random	Family (category x locality)	0.0	0.9
			Individual tree (category x locality x family)	78.7	<0.0001
Placerville	Specific leaf area	Fixed	Maternal climate category	$0.54_{2,\ 57.2}$	0.6
			Locality (category)	$1.06_{6,\ 57.3}$	0.4
		Random	Family (category x locality)	0.0	0.9
			Individual tree (category x locality x family)	40.9	<0.0001
	Leaf dissection	Fixed	Maternal climate category	$0.3_{2,\ 9.11}$	0.7
			Locality (category)	$1.66_{6,\ 8.91}$	0.2
		Random	Family (category x locality)	2.4	0.06
			Individual tree (category x locality x family)	43.2	<0.0001

random effects. The significance of random effects was tested using likelihood-ratio tests (Littel et al. 1996). To correct for heteroscedasticity, analyses were conducted using natural log-transformed values of leaf dissection, although means are reported below on the untransformed scale. Specific leaf area required no transformation to meet model assumptions. Separate statistical models were used for data collected from each site (Chico and Placerville). Significant differences in leaf traits among climate categories were considered consistent with the hypothesis that leaf shape evolves in response to local climate. For the Chico dataset focused on carbon assimilation and leaf morphology, variation in *A* (carbon assimilation) was regressed against leaf dissection using a mixed-model nested ANCOVA. Sampling date and leaf dissection were included as fixed effects, and individual tree was included as a random effect. The sampling date x leaf dissection fixed effect interaction term did not significantly explain variation in *A* ($P > 0.6$), indicating that the effect of leaf dissection on *A* did not vary among sampling dates, so it was removed from the final model. Leaf dissection and *A* were both natural log-transformed prior to analysis to correct for heteroscedasticity. A significantly positive relationship between leaf dissection and *A* was considered consistent with the hypothesis that greater leaf dissection is associated with higher photosynthetic rates.

RESULTS

Leaf dissection and specific leaf area varied widely among sampled leaves (coefficient of variation [CV] for specific leaf area = 28.4 and 19.0 for Placerville and Chico, respectively; for leaf dissection, CV = 29.8 and 25.4 for Placerville and Chico, respectively). Nonetheless, neither trait varied significantly among categories of maternal multivariate climatic characteristics at either site (Table 1; Fig. 2).

The subsampling of trees for measuring *A* was successful at capturing variation in leaf dissection within Chico. The CV of maternal mean leaf dissection values from the full dataset measured in 2016 was 13.6 (MacDonald 2017), whereas the CV from our 2018 subsample of 18 maternal mean leaf dissection values was 19.6. In addition, maternal mean leaf dissection scores were positively correlated across the two datasets ($r_s = 0.71$, $P = 0.0009$, $n = 18$), validating our assumption that measurements of leaf dissection on trees in 2016 would predict measurements during 2018. Carbon assimilation increased significantly with leaf dissection among sampled trees (Table 2; Fig. 3; Slope = 0.86). In addition, estimates of *A* declined over the sampling period, possibly reflecting increasing air temperature and water limitation during the early summer sampling period (Table 2; Fig. 3).

TABLE 2. MIXED MODEL ANALYSIS OF COVARIANCE TESTING THE EFFECTS OF LEAF DISSECTION ($\text{MM} \cdot \text{MM}^{-2}$) AND SAMPLING DAY ON CARBON ASSIMILATION ($\mu\text{MOL CO}_2 \cdot \text{M}^{-2} \cdot \text{S}^{-1}$) IN *QUERCUS LOBATA* GROWING IN A COMMON GARDEN EXPERIMENT AT CHICO. Twenty-eight saplings (17 families) were subsampled to maximize variation in leaf dissection (see Methods). *F*-tests of fixed effects and χ^2 value from a likelihood-ratio test of the random effect are shown.

Effect type	Source	$F_{\text{ndf, ddf}}$ or χ^2	*P*
Fixed	Leaf dissection	$5.13_{1,\ 43.4}$	0.03
	Sampling day	$9.5_{5,\ 20.3}$	<0.0001
Random	Individual Tree	8.6	0.003

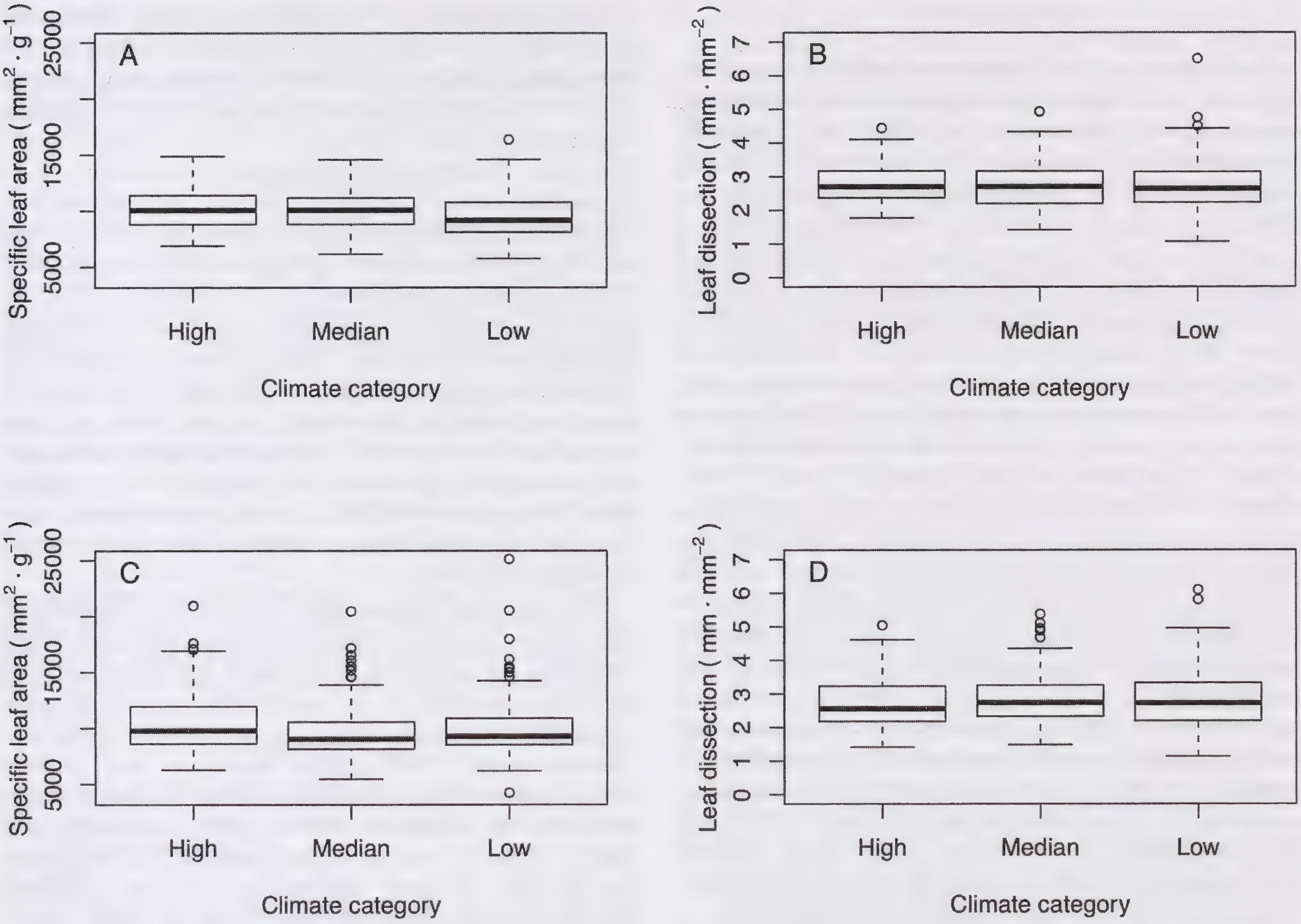

FIG. 2. Tukey's box plots of specific leaf area and leaf dissection (perimeter · area^{-1}) among leaves collected from *Quercus lobata* grown in common gardens in Chico (A and B) and Placerville, California (C and D) as a function of multivariate climatic characteristics of the maternal seed source (see Methods). See Table 1 for results of statistical tests.

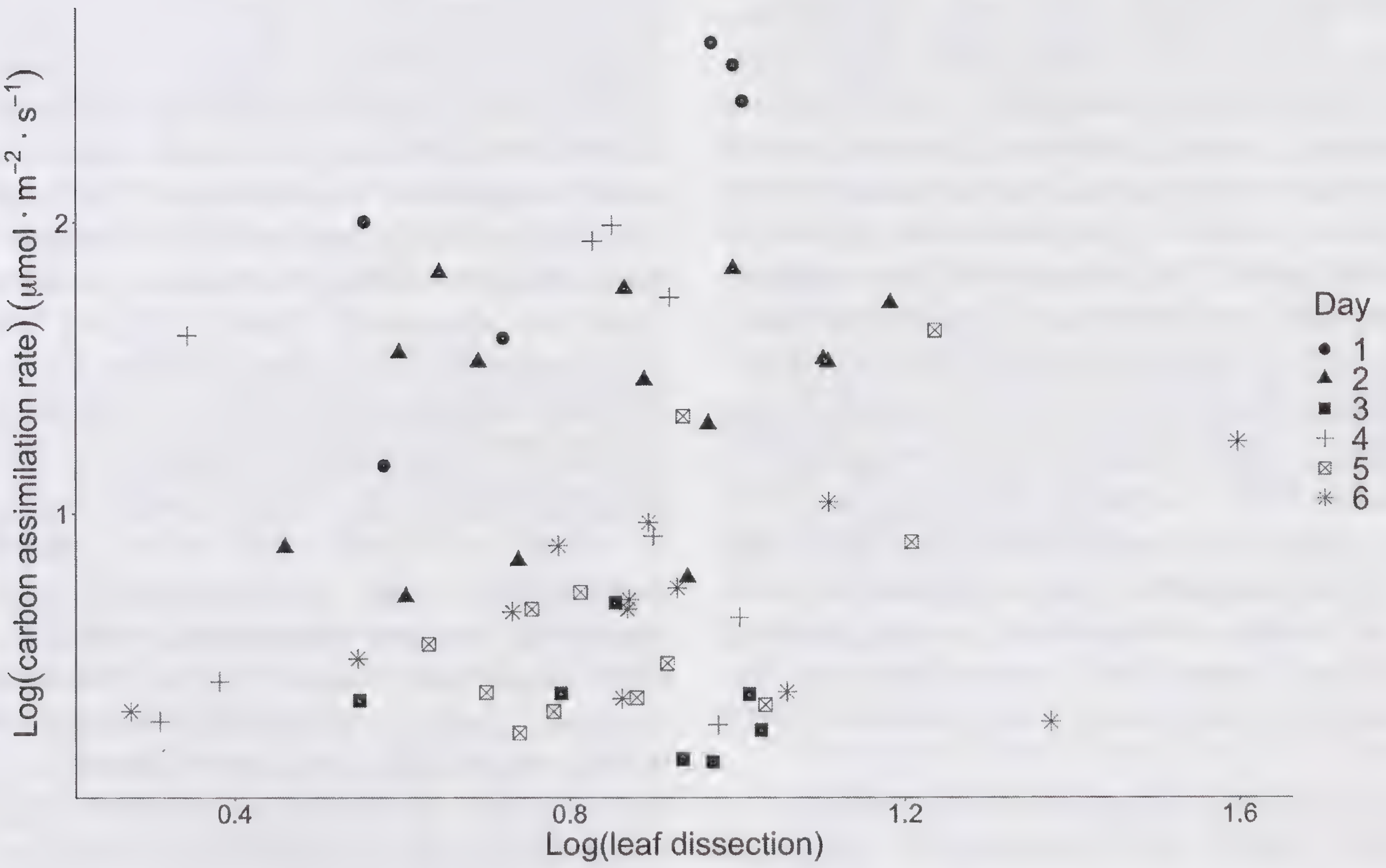

FIG. 3. Carbon assimilation as a function of leaf dissection (perimeter · area^{-1} in mm · mm^{-2}) in *Quercus lobata* sampled at the Chico common garden site. Sampling day was included in the model as a covariate. Carbon assimilation and dissection were log-transformed for analysis (see Methods). See Table 2 for results of statistical tests.

DISCUSSION

Oak leaves are well known to harbor tremendous variation in shape. We explored two hypotheses associated with that variation. First, we tested the hypothesis that variation in leaf shape among populations is a consequence of adaptation to prevailing climatic conditions. Previous studies have reported that leaf morphological traits, including leaf dissection, vary with climate and other site characteristics (Ogaya and Peñuelas 2007; Peppe et al. 2011; Royer 2012; Albarrán-Lara et al. 2015; Riordan et al. 2016; MacDonald 2017). If this hypothesis were true, we would expect variation in leaf morphology among trees in the common garden to be associated with the climatic conditions of the maternal source trees, because of inherited leaf morphological variations from the maternal trees. We instead found that the wide variation in leaf morphology observed was not associated with variation in climate, thus failing to support this hypothesis (Fig. 2). This may indicate that leaf dissection is principally influenced by the environment. Trait plasticity in response to climate may itself be adaptive in variable environments and could facilitate species persistence in response to climate change in circumstances where adaptive evolution is slow (Hoffmann and Sgrò 2011; but see MacDonald 2017). On the other hand, phenotypic variation in leaf morphology may be genetically controlled, but not associated with adaptation to climate. MacDonald (2017), in a much larger study of leaf morphology within the common garden, reported significant variation among family lines for leaf dissection and specific leaf area, which suggests that variation is genetically based.

The extent to which leaf morphological variation in natural populations of *Q. lobata* is associated with climate is unclear, although the data herein may provide additional insight into this hypothesis. Albarrán-Lara et al. (2015) examined phenotypic variation in *Q. lobata* leaves sampled from 127 adults distributed among three elevational transects and found substantial morphological variation, although climatic variation within transects was relatively small. Leaf thickness in the progeny of the sampled trees was positively correlated with maximum temperature of the site of maternal trees (Albarrán-Lara et al. 2015). Other studies of oaks have reported that leaf morphology varies adaptively in response to climate (Abrams 1990; Cavender-Bares et al. 2004; Riordan et al. 2016; but see Royer et al. 2008). We suggest that study of phenotypic variation in field populations of valley oak across its range may provide additional insight into the validity of the hypothesis that leaf morphology is associated with climate.

Second, we tested the hypothesis that variation in leaf shape has a functional consequence for plant physiology. We found that more dissected leaves had higher photosynthetic rates (Fig. 3), which is consistent with this hypothesis. Carbon assimilation (*A*) measurements were collected during June and July, and *A* decreased over the period during which data were collected. California's central valley, where Chico is located, has a very hot, dry season typically beginning in May; during the study no precipitation fell and temperatures routinely exceeded 35°C (University of California, Division of Agriculture and Natural Resources 2019). Even though the site was irrigated for one day during the time we collected *A* measurements (see Methods), the intensity of water stress experienced by the trees may have increased throughout this period. We avoided collecting *A* measurements for four days following the irrigation event to minimize its impact on our data. In any event, declines in *A* with increasing water stress are not uncommon (Chaves 1991; Osakabe et al. 2014), thus the temporal decline in *A* that we observed may have been a consequence of increased water stress experienced by trees.

The positive relationship between leaf dissection and *A* may be a consequence of water relations. Prior research, for example, has found variation in leaf dissection in oaks to be negatively associated with hydraulic resistance (Sisó et al. 2001). Similarly, Nicotra et al. (2008) found higher *A* and greater water loss in leaves of *Pelargonium* that were more dissected. In addition, other studies have suggested that a dissected morphology improves air exchange across leaf surfaces, leading to a more efficient transfer of heat (Gurevitch and Schuepp 1990). Thus, as early summer became increasingly hot, individual trees with more dissected leaves may have experienced reduced water stress, and consequently, these individuals may have been able to maintain higher photosynthetic rates under dry conditions than trees with less dissected leaves. Although we were not able to collect these data during the current study, this idea could be tested by concurrent collection of plant water potential and carbon assimilation measurements in trees with a range of leaf dissection values.

This study provides evidence that variation in leaf shape found among valley oak individuals within the common garden is associated with photosynthetic rate. In addition, our results show that factors other than maternal climate influence variation in the leaf traits we measured. Some of these factors may be environmental, as the traits we measured are known to hold substantial phenotypic plasticity; MacDonald (2017), for example, found leaf dissection to be the most plastic of five leaf traits measured. Studies of other oak taxa also report plasticity in leaf morphology that is associated with functional responses to environmental variation (Wu et al. 2016; Kusi and Karsai 2019). Within the *Q. lobata* common garden, genetically based variation in leaf morphology has also been reported (MacDonald 2017). Oaks are known to harbor variation in leaf traits that involve adaptations to climate (Cavender-Bares 2004; Ramírez-Valiente et al. 2017a; Mead et al. 2019). Variation in leaf shape within valley oaks, whether plastic or genetic, appears to play a functional role in mitigating environmental stress and climatic variation. Our results suggest future studies exploring the functional consequences of variation in leaf shape would be productive.

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LITERATURE CITED

ABRAMS, M. D. 1990. Adaptations and responses to drought in *Quercus* species of North America. Tree Physiology 7:227–238.

ACKERLY, D. D., S. A. DUDLEY, S. E. SULTAN, J. SCHMITT, J. S. COLEMAN, C. R. LINDER, D. R. SANDQUIST, M. A. GEBER, A. S. EVANS, T. E. DAWSON, AND M. J. LECHOWICZ. 2000. The evolution of plant ecophysiological traits: recent advances and future directions. Bioscience 50:979–995.

ALBARRÁN-LARA, A. L., J. W. WRIGHT, P. F. GUGGER, A. DELFINO-MIX, J. M. PEÑALOZA-RAMÍREZ, AND V. L. SORK. 2015. Phenotypic variation in California populations of valley oak (*Quercus lobata* Née) sampled along elevational gradients. Pp. 433–445 *in* R. B. Standiford and K. L. Purcell (eds.), Proceedings of the seventh California oak symposium: managing oak woodlands in a dynamic world. General Technical Report PSW-GTR-251. USDA Forest Service, Pacific Southwest Research Station, Albany, CA.

ARNTZ, A. M., E. H. DELUCIA, AND N. JORDAN. 2000. From fluorescence to fitness: variation in photosynthetic rate affects fecundity and survivorship. Ecology 81:2567–2576.

BROWNE, L., J. W. WRIGHT, S. FITZ-GIBBON, P. F. GUGGER, AND V. L. SORK. 2019. Adaptational lag to temperature in valley oak (*Quercus lobata*) can be mitigated by genome-informed assisted gene flow. Proceedings of the National Academy of Sciences. 116:25179–25185.

CAVENDER-BARES, J., K. KITAJIMA, AND F. A. BAZZAZ. 2004. Multiple trait associations in relation to habitat differentiation among 17 Floridian oak species. Ecological Monographs 74:635–662.

CHAVES, M. M. 1991. Effects of water deficits on carbon assimilation. Journal of Experimental Botany 42:1–16.

DELFINO-MIX, A., J. W. WRIGHT, P. F. GUGGER, C. LIANG, AND V. L. SORK. 2015. Establishing a range-wide provenance test in valley oak (*Quercus lobata* Née) at two California sites. Pp. 413–424 *in* R. B. Standiford and K. L. Purcell (eds.), Proceedings of the seventh California oak symposium: managing oak woodlands in a dynamic world. General Technical Report PSW-GTR-251. USDA Forest Service, Pacific Southwest Research Station, Albany, CA.

DUTECH, C., V. L. SORK, A. J. IRWIN, P. E. SMOUSE, AND F. W. DAVIS. 2005. Gene flow and fine-scale genetic structure in a wind-pollinated tree species, *Quercus lobata* (Fagaceae). American Journal of Botany 92:252–261.

FERRIS, K. G. 2019. Endless forms most functional: uncovering the role of natural selection in the evolution of leaf shape. American Journal of Botany 106:1532–1535.

GIVNISH, T. J. 1978. Ecological aspects of plant morphology: leaf form in relation to environment. Acta Biotheoretica 11:83–142.

GRIVET, D., P. E. SMOUSE AND V. L. SORK. 2005. A novel approach to an old problem: tracking dispersed seeds. Molecular Ecology 14:3585–3595.

GRIVET, D., J. J. ROBLEDO-ARNUNCIO, P. E. SMOUSE AND V. L. SORK. 2009. Relative contribution of contemporary pollen and seed dispersal to the effective parental size of seedling population of California valley oak (*Quercus lobata*, Née). Molecular Ecology 18:3967–3979.

GUGGER, P. F., M. IKEGAMI, AND V. L. SORK. 2013. Influence of late Quaternary climate change on present patterns of genetic variation in valley oak, *Quercus lobata* Née. Molecular Ecology 22:3598–3612.

GUREVITCH, J. AND P. H. SCHUEPP. 1990. Boundary layer properties of highly dissected leaves: an investigation using an electrochemical fluid tunnel. Plant, Cell, and Environment 13:783–792.

HOFFMANN, A. A. AND C. M. SGRÒ. 2011. Climate change and evolutionary adaptation. Nature 470:479–486.

JENSEN, R. T. 1990. Detecting shape variation in oak leaf morphology: A comparison of rotational-fit methods. American Journal of Botany 77:1279–1293.

KOLB, T. E., K. C. STEINER, AND L. H. MCCORMICK. 1990. Growth response of northern red-oak and yellow-poplar seedlings to light, soil moisture and nutrients in relation to ecological strategy. Forest Ecology and Management 38:65–78.

KUEPPERS, L. M., M. A. SNYDER, L. C. SLOAN, E. S. ZAVALETA, AND B. FULFROST. 2005. Modeled regional climate change and California endemic oak ranges. Proceedings of the National Academy of Sciences 102:16281–16286.

KUSI, J. AND I. KARSAI. 2019. Plastic leaf morphology in three species of *Quercus*: the more exposed leaves are smaller, more lobated, and denser. Plant Species Biology doi.org/10.1111/1442-1984.12253.

LITTELL, R. C., G. A. MILLIKEN, W. W. STROUP, AND R. D. WOLFINGER. 1996. SAS system for mixed models. SAS Institute, Cary, NC.

MACDONALD, B. W. S. 2017. Local climatic heterogeneity predicts differences in phenotypic plasticity across populations of a widely-distributed oak species. M.S. thesis. University of California, Los Angeles, CA.

MCLAUGHLIN, B. C. AND E. S. ZAVALETA. 2012. Predicting species responses to climate change: demography and climate microrefugia in California valley oak (*Quercus lobata*). Global Change Biology 18:2301–2312.

MEAD, A., J. PEÑALOZA RAMIREZ, M. K. BARTLETT, J. W. WRIGHT, L. SACK, AND V. L. SORK. 2019. Seedling response to water stress in valley oak (*Quercus lobata*) is shaped by different gene networks across populations. Molecular Ecology 28:5248–5264.

Meyer, V. C. 2002. Soil moisture availability as a factor affecting valley oak (*Quercus lobata* Neé) seedling establishment and survival in a riparian habitat, Cosumnes River Preserve, Sacramento County, California. Pp. 551–564 *in* R. B. Standiford, D. McCreary, and K. L. Purcell (eds.), Proceedings of the fifth symposium on oak woodlands: oaks in California's changing landscape. General Technical Report PSW-GTR-184. USDA Forest Service, Pacific Southwest Research Station, Albany, CA.

Nicotra, A. B., M. J. Cosgrove, A. Cowling, C. D. Schlichting, and C. S. Jones. 2008. Leaf shape linked to photosynthetic rates and temperature optima in South African *Pelargonium* species. Oecologia 154:625–635.

Nicotra, A. B., A. Leigh, C. K. Boyce, C. S. Jones, K. J. Niklas, D. L. Royer, and H. Tsukaya. 2011. The evolution and functional significance of leaf shape in the angiosperms. Functional Plant Biology 38:535–552.

Ogaya, R. and J. Peñuelas. 2007. Leaf mass per area ratio in *Quercus ilex* leaves under a wide range of climatic conditions. The importance of low temperatures. Acta Oecologica 31:168–173.

Osakabe, Y., K. Osakabe, K. Shinozaki, and L.S. Tran. 2014. Response of plants to water stress. Frontiers in Plant Science 5:1–8.

Peppe, D. J., D. L. Royer, B. Cariglino, S. Y. Oliver, S. Newman, E. Leight, G. Enikolopov, M. Fernandez-Burgos, F. Herrera, J. M. Adams, E. Correa, E. D. Currano, J. M. Erickson, L. F. Hinojosa, J. W. Hoganson, A. Iglesias, C. A. Jaramillo, K. R. Johnson, G. J. Jordan, N. J. Kraft, E. C. Lovelock, C. H. Lusk, Ü. Niinemets, J. Peñuelas, G. Rapson, S. L. Wing, and I. J. Wright. 2011. Sensitivity of leaf size and shape to climate: global patterns and paleoclimatic applications. New Phytologist 190:724–739.

Ramírez-Valiente, J. A., A. Center, J. P. Sparks, K. L. Sparks, J. R. Etterson, T. Longwell, G. Pitz, and J. Cavender-Bares. 2017a. Population-level differentiation in growth rates and leaf traits in seedlings of the neotropical live oak *Quercus oleoides* grown under natural and manipulated precipitation regimes. Frontiers in Plant Science 8:585.

Ramírez-Valiente, J. A., N. J. Deacon, J. Etterson, A. Center, J. P. Sparks, K. L. Sparks, T. Longwell, G. Pilz, and J. Cavender-Bares. 2017b. Natural selection and neutral evolutionary processes contribute to genetic divergence in leaf traits across a precipitation gradient in the tropical oak *Quercus oleiodes*. Molecular Ecology 27:2176–2192.

Riordan, E. C., P. F. Gugger, J. Ortego, C. Smith, K. Gaddis, P. Thompson, and V. L. Sork. 2016. Association of genetic and phenotypic variability with geography and climate in three southern California oaks. American Journal of Botany 103:73–85.

Royer, D. L. 2012. Leaf shape responds to temperature but not CO_2 in *Acer rubrum*. PLoS ONE 7:e49559.

Royer, D. L., J. C. McElwain, J. M. Adams, and P. Wilf. 2008. Sensitivity of leaf size and shape to climate within *Acer rubrum* and *Quercus kelloggii*. New Phytologist 179:808–817.

Schneider, C. A., W. S. Rasband, and K. W. Eliceiri. 2012. NIH Image to ImageJ: 25 years of image analysis. Nature Methods 6:671–675.

Sisó, S., J. J. Camarero, and E. Gil-Pelegrín. 2001. Relationship between hydraulic resistance and leaf morphology in broadleaf *Quercus* species: a new interpretation of leaf lobation. Trees 15:341–345.

Sork, V. L., P. E. Smouse, D. Grivet and D. G. Scofield. 2015. Impact of asymmetric male and female gamete dispersal on allelic diversity and spatial genetic structure in valley oak (*Quercus lobata* Née). Evolutionary Ecology 29:927–945.

Sork, V. L., F. W. Davis, P. E. Smouse, V. J. Apsit, R. J. Dyer, J. F. Fernandez-M and B. Kuhn. 2002. Pollen movement in declining populations of California Valley oak, *Quercus lobata*: Where have all the fathers gone? Molecular Ecology 11:1657–1668.

Sork, V. L., K. Squire, P. F. Gugger, S. E. Steele, E. D. Levy, and A. J. Eckert. 2016. Landscape genomic analysis of candidate genes for climate adaptation in a California endemic oak, *Quercus lobata*. American Journal of Botany 103:33–46.

Sork, V. L., F. W. Davis, R. Westfall, A. Flint, M. Ikegami, H. Wang, and D. Grivet. 2010. Gene movement and genetic association with regional climate gradients in California valley oak (*Quercus lobata* Née) in the face of climate change. Molecular Ecology 19:3806–3823.

Tyler, C. M., B. Kuhn, and F. W. Davis. 2006. Demography and recruitment limitations of three oak species in California. Quarterly Review of Biology 81:127–152.

University of California, Division of Agriculture and Natural Resources. 2019. Durham, Chico - monthly totals. Website http://cebutte.ucanr.edu/About_Us/Weather/?weather=station&station=12 [accessed 5 July 2019]

Valladares, F., E. Martinez-Ferri, L. Balaguer, E. Perez-Corona, and E. Manrique. 2000. Low leaf-level response to light and nutrients in Mediterranean evergreen oaks: a conservative resource-use strategy? The New Phytologist 148:79–91.

Wang T., A. Hamann, D. Spittlehouse, and C. Carroll. 2016. Locally downscaled and spatially customizable climate data for historical and future periods for North America. PLoS ONE 11:e0156720.

Westerband, A. C. and C. C. Horvitz. 2017. Photosynthetic rates influence the population dynamics of understory herbs in stochastic light environments. Ecology 98:370–381.

Whipple, A. A., R. M. Grossinger, and F. W. Davis. 2011. Shifting baselines in a California oak savanna: nineteenth century data to inform restoration scenarios. Restoration Ecology 19:88–101.

Wright, I. J., P. B. Reich, J. H. Cornelissen, D. S. Falster, P. K. Groom, K. Hikosaka, W. Lee, C. H. Lusk, Ü. Niinemets, J. Oleksyn, N. Osada, H. Poorter, D. I. Warton, and M. Westoby. 2005. Modulation of leaf economic traits and trait relationships by climate. Global Ecology and Biogeography 14: 411–421.

Wu, T., P. Zhang, L. Zhang, G. G. Want, M. Yu. 2016. Morphological response of eight *Quercus* species to simulated wind load. PLoS ONE 11:e0163613.

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AN UPDATED DATABASE OF SERPENTINE ENDEMISM IN THE CALIFORNIA FLORA

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Abstract

We update and revise the serpentine affinity database of Safford et al. (2005), which documents levels of plant taxon association with ultramafic ("serpentine") substrates in the California flora. The revised database reflects recent taxonomic changes consistent with the second edition of the Jepson Manual (TJM2) and more recent updates to the Jepson eFlora, and includes additional species that were not previously documented as serpentine associates. We also include serpentine-associated species that have been described since the publication of TJM2 and are not yet incorporated in the eFlora. A number of taxa were removed from the Safford et al. (2005) database due to new ecological information or taxonomic changes. As before, the new database presents information on rarity, geographic distribution, taxonomy, and lifeform. Based on our new database numbers and TJM2's list of California endemic species, the percentage of California endemic full species that are +/– restricted to ultramafic substrates has risen to 14.7%. Of 255 total endemic taxa in our database (including strict and "broad" endemics), 148 (c. 60%) come from only ten plant families, concentrated mostly in one or two genera per family. The North Coast and Klamath Ranges continue to support more serpentine endemics than the rest of the State combined. The previous version of the database has been widely used in biodiversity research and conservation management, and we hope that this improved and updated version will prove as valuable.

Key Words: California flora, edaphic, endemics, serpentine, ultramafic.

Soils derived from ultramafic parent materials–often referred to as "serpentine"–support a great diversity of plant life in California. Serpentine soils are generally ecologically stressful environments because they are poor in plant macronutrients, have high magnesium : calcium ratios, and contain toxic heavy metals (Alexander et al. 2007). Serpentine environments support high levels of native plant diversity partly because they are less likely to support the (often non-native) dominant species that competitively exclude other plants on more fertile substrates (Brooks 1987). In addition, the stressful environment of serpentine leads to high levels of endemism. While serpentine soils occupy less than 1.5% of California's geographic area (Harrison et al. 2000), a high number of California's endemic plant species are partially or entirely restricted to serpentine soils (described below, also see Safford et al. 2005; Safford 2011). Understanding the plant diversity associated with serpentine environments is important for facilitating research into basic ecological and evolutionary questions (of which there is a long history in California serpentine; Harrison and Rajakaruna 2011), as well as for informing management decisions involving landscapes, natural disturbances, and conservation (Safford and Harrison 2004, 2008).

To this point, the serpentine endemism database of Safford et al. (2005) has provided the most comprehensive documentation of plant species affinities for serpentine substrates in California. This database assigns plant taxa a ranking representing their degree of specialization to serpentine soils based on herbarium records, botanical descriptions, field data, expert opinion, and published literature. The database has been widely used for a variety of purposes since its publication. The rankings have been cited by numerous ecological and evolutionary studies, such as research on the evolutionary origins of serpentine adaptation (Anacker et al. 2010), biogeographic considerations of plant diversity and endemism in the California flora (Harrison et al. 2006; Burge et al. 2011), autoecological studies of serpentine species (Eckert 2006), and studies of mycorrhizae on serpentine soils (Southworth et al. 2014). The serpentine affinity rankings have been integrated into the CalFlora (http://www.calflora.org) web interface—a database on California plants—where the rankings are displayed on the pages of serpentine-associated species. The serpentine database has also been used by land managers in conservation planning, environmental assessments and impact statements, and resource management plans.

Methods

Our understanding of the systematics and ecology of the California flora has expanded substantially since the earlier version of this database was

TABLE 1. TAXA DROPPED FROM SERPENTINE AFFINITY DATABASE AFTER 2012. TJM2 (Baldwin et al. 2012) included many taxonomic changes and new taxa. These changes were incorporated into the database at the time of TJM2. This table includes taxa dropped from the list since that time.

Species	Family	Reason and source
Chlorogalum purpureum var. *reductum* Hoover	Agavaceae	Taxon does not grow on serpentine soils (Kofron et al. 2013)
Cardamine pachystigma var. *pachystigma* (S. Watson) Rollins	Brassicaceae	Taxon is not a serpentine indicator; reanalysis of herbarium and collection records
Sedum obtusatum ssp. *obtusatum* A. gray.	Crassulaceae	Taxon is not a serpentine indicator; reanalysis of herbarium and collection records
Carex amplectens Steud.	Cyperaceae	Moved to *Carex fracta* Mack. by Baldwin et al. (2012), which is not a serpentine indicator
Swertia fastigiata Pursh	Gentianaceae	Moved to *Frasera umquaensis* M. Peck & Applegate by Baldwin et. al (2012), which is not a serpentine indicator
Calochortus greenei S. Watson	Liliaceae	Taxon does not grow on serpentine soils; government agency (BLM, USFWS) reports on species ecology
Ceanothus papillosus Torr. & A. Gray var. *roweanus* McMinn	Rhamnaceae	Taxon not recognized by TJM2 or Jepson eFlora, herbarium collections and CalFlora observations do not support taxon as serpentine indicator
Brodiaea pallida Hoover	Themidaceae	New collections show that only 1 of 5 population groups occurs on serpentine; R. Preston, UC Davis, pers. comm.
Brodiaea purdyi Eastw.	Themidaceae	Taxon subsumed within *B. minor* (Benth.) S. Watson, which is not a serpentine indicator (Preston 2006; Baldwin et al. 2012)

published. Here, we provide a revised version of the database (Appendix 1; Supplemental Table 1), with nomenclature updated to reflect The Jepson Manual, 2nd edition (TJM2; Baldwin et al. 2012) and then again using the most recent Jepson eFlora (most recent version accessed November 18, 2019; Jepson Flora Project 2019). This contribution follows on Safford (2011), which provided a lay person's summary of the status of the endemism database just as TJM2 was being prepared for press. The general patterns discussed in Safford (2011) are still valid, but it was important to incorporate the published results from Baldwin et al. (2012) and the most recent Jepson eFlora (Jepson Flora Project 2019), and to provide a completely revised version of the database itself, which was not part of Safford (2011).

In the current database (Appendix 1), we have added numerous additional species that were not included on the original 2005 list, many of which are recently described serpentine-associated species. We also removed seven taxa from the list that we constructed after TJM2 (Table 1) because recent taxonomic changes and/or further study has indicated they are not strongly associated with serpentine substrates. To revise the original list, we first updated nomenclature to current Jepson eFlora names (as of November 18, 2019; Jepson Flora Project 2019). We then solicited feedback on the list from numerous expert California botanists and requested suggestions for additional species that should be included. We also conducted a literature review for recently described species that have affinities for serpentine. We then conducted further research on all species that were identified by experts or through the literature review as possibilities for addition to or removal from the list, as described below.

We have ranked new additions to the list using the same semi-quantitative scale as the original database (see Safford et al. 2005 for details), with the difference that we have reduced all rankings >6 to 6, as those resulted from the addition of CalFlora information (which at the time could be considered independent of our other sources). Today CalFlora directly references the serpentine affinity database in its species descriptions. Rankings of new additions to the list presented here are based primarily on herbarium records (mostly accessed via the Consortium of California Herbaria (CCH1 2019; CCH2 2019), habitat descriptions by Baldwin et al. (2012) and the Jepson eFlora (Jepson Flora Project 2019), CalFlora observation records (CalFlora 2019), the primary literature, and in some cases, direct input from botanical experts. In the CCH herbarium records, we accessed at least 150 collection records for each taxon (except where records totaled <150, in which case we accessed all records), using random selection where necessary to ensure no bias in regional coverage. Where CCH or CalFlora records were <5, we combined the two and treated them as a single information source. We used the Berkeley Mapper (linked to the CCH website), Google Earth, our field experience, and various geologic and jurisdictional (e.g., US Forest Service) maps to visualize the locations of herbarium records and to determine, when possible, whether botanical records lacking geological information were found on or off of ultramafic substrates. Taxa with >50% of usable records ("usable" = the records identified the substrate, or we were able to determine the substrate by another fashion) from serpentine made their way

TABLE 2. TAXA INCLUDED IN THE SERPENTINE AFFINITY LIST THAT ARE NOT IN THE CURRENT JEPSON EFLORA (AS OF NOVEMBER 18, 2019). These include recently described taxa as well as taxa that are widely recognized by botanists in California, but are not included in the current eFlora because of taxonomic uncertainty.

Taxon	Source
Brodiaea rosea ssp. *rosea* (Greene) Baker	Preston 2013
Calystegia vanzuukiae Brummitt & Namoff	Brummitt and Namoff 2013
Cardamine pachystigma var. *dissectifolia* (S. Watson) Rollins	R. Preston and L. Janeway, pers comm and CCH and CalFlora records
Claytonia serpenticola T.R. Stoughton	Stoughton 2017
Dicentra formosa ssp. *oregana* (Haw.) Walp.	Baldwin et al. 2012; L. Hoover, U.S. Forest Service, pers. comm.
Erythranthe willisii G.L. Nesom	Nesom 2017
Hesperolinon sharsmithiae R. O'Donnell	O'Donnell 2006
Sedum eastwoodiae (Britton) A. Berger	Zika et al. 2018
Sedum flavidum B.L. Wilson & Zika	Zika et al. 2018
Sedum kiersteadiae B.L. Wilson & R.E. Brainerd	Wilson et al. 2014
Sedum patens Zika	Zika et al. 2018
Sedum rubiginosum Zika & B.L. Wilson	Zika et al. 2018
Vaccinium coccineum Piper	L. Hoover and J. Nelson, U.S. Forest Service, pers comm.

onto the final list. Rankings of new list additions (e.g., recently described species) should be used cautiously since many of them are based on limited data, and we suggest that all species ranked based on three or fewer sources are in need of further study. All species in the updated list follow the nomenclature of the current (November 2019) Jepson eFlora except for 13 taxa (Table 2), most of which are recently described.

We emphasize that we did not carry out a complete search of new collection records for every taxon since 2005. This was only carried out for taxa where recent publications, taxonomic changes, or personal communications from California botanists led us to believe that such a search might change the status of the species. For new additions to the list, we no longer required three separate sources of information supporting their affinity for serpentine if evidence for their affinity to serpentine appeared strong (for example, in the herbarium records).

Finally, it is important to note that for species for which *all* described infraspecific taxa (subspecies, varieties) exhibit the same level of serpentine affinity, we only include the full species name in our database.

RESULTS AND DISCUSSION

As in Safford et al. (2005) and Safford (2011), we define serpentine endemic taxa as those that scored at least 4.5 in our ranking process. Put another way, our class of "serpentine endemics" includes strict endemics (more than c. 95% of recorded occurrences on ultramafics) and broad endemics (c. 85–94%). The updated serpentine affinity database (Appendix 1) contains 255 endemic taxa (strict plus broad endemics), 193 of which are full species (this includes five species for which all of the subspecies are listed in the database due to differing levels of serpentine affinity: *Arctostaphylos bakeri* Eastw., *A. montana* Eastw., *Calystegia collina* (Greene) Brummitt, *Cirsium fontinale* (Greene) Jeps., and *Lessingia micradenia* Greene). Thus, serpentine endemic species account for about 14.7% – more than 1/7 – of the endemic species in California (based on 1315 endemic species in Baldwin 2012). This is a notable increase from the 12.5% reported by Safford et al. (2005), and is due to additions of newly described species and a decrease in the number of California endemic species according to Baldwin et al. (2012).

Taxonomic revisions have led to some changes from Safford et al. (2005) in the ordering of family and genera with the most serpentine endemic taxa. Asteraceae remains the family with the most serpentine endemics, with 25 strict endemics, 13 broad endemics, and 106 total serpentine-associated taxa (Table 3). Liliaceae, which historically contained the second most serpentine endemics of any family (considering both strict and broad endemics), has been split into several smaller families, many of which are further down the current list, including Alliaceae – also in the top ten families, Agavaceae, Themidaceae, and so on. As a result, Brassicaceae is now the second most endemic-rich family (Table 3). Scrophulariaceae was also split in Baldwin et al. (2012) into numerous plant families, and it has dropped from a fifth place ranking in the Safford et al. (2005) rankings to a complete absence from the list now. Families derived from Scrophulariaceae are still important components of serpentine endemism in California however: for example, Orobanchaceae currently occupies sixth place on the list, and Phrymaceae and Plantaginaceae are further down the list. *Eriogonum* is now the most endemic-rich genus, followed by *Streptanthus* (Table 4).

As discussed by Safford et al. (2005; see their Figs 1 and 2), the distribution of taxa among plant families and genera is very different when comparing serpentine endemics and California endemics. Families which support many more serpentine endemic taxa than expected include Linaceae, Polygonaceae,

TABLE 3. NUMBERS OF SERPENTINE ENDEMIC AND NEAR ENDEMIC TAXA BY FAMILY. [1] Strict endemics. [2] Strict endemics plus broad endemics ("endemic taxa" in this paper). [3] Strict and broad endemics plus "near endemic" taxa (taxa transitional from strong indicators to broad endemics). [4] Total taxa in our database, including weak indicators and taxa transitional from indifferent to weak indicators. Families ranked by numbers of endemics (strict + broad).

	Serpentine affinity score			
Family	≥5.5[1]	≥4.5[2]	≥3.5[3]	Total[4]
Asteraceae	25	38	46	106
Brassicaceae	19	24	28	38
Polygonaceae	11	19	22	41
Liliaceae	5	13	16	38
Polemoniaceae	9	10	11	21
Orobanchaceae	7	10	10	19
Apiaceae	7	9	12	33
Crassulaceae	8	9	9	16
Linaceae	8	9	9	14
Ericaceae	5	8	10	15
Fabaceae	4	7	11	25
Alliaceae	4	7	11	24
Lamiaceae	6	7	9	17
Boraginaceae	6	6	11	24
Caryophyllaceae	5	6	8	18
Campanulaceae	3	5	8	13
Rhamnaceae	4	5	7	14
Onagraceae	3	5	7	13
Cyperaceae	3	5	7	12
Convolvulaceae	1	5	6	7
Phrymaceae	4	4	6	8
Rubiaceae	3	4	4	8
Montiaceae	0	3	6	17
Rosaceae	1	3	6	11
Plantaginaceae	1	3	5	15
Poaceae	1	3	3	18
Iridaceae	2	3	3	5
Violaceae	0	2	3	7
Cupressaceae	0	2	3	6
Malvaceae	2	2	2	7
Agavaceae	2	2	2	5
Salicaceae	2	2	2	3
Gentianaceae	2	2	2	2
Garryaceae	1	2	2	2
Themidaceae	0	1	5	8
Ranunculaceae	1	1	3	7
Papaveraceae	0	1	1	5
Berberidaceae	1	1	1	4
Pteridaceae	0	1	1	4
Fagaceae	1	1	1	3
Orchidaceae	0	1	1	3
Dryopteridaceae	1	1	1	2
Lentibulariaceae	1	1	1	1
Apocynaceae	1	1	1	1
Verbenaceae	0	1	1	1
Melanthiaceae	0	0	2	4
Pinaceae	0	0	1	6
Parnassiaceae	0	0	1	2
Saxifragaceae	0	0	1	1
Sarraceniaceae	0	0	1	1
Tecophilaeaceae	0	0	0	1
Primulaceae	0	0	0	1
Polygalaceae	0	0	0	1
Cistaceae	0	0	0	1

TABLE 4. GENERA WITH MORE THAN THREE TAXA ENDEMIC TO SERPENTINE (MEAN AFFINITY SCORE ≥ 4.5).

Genus	Family	Number of taxa
Eriogonum	Polygonaceae	19
Streptanthus	Brassicaceae	18
Allium	Alliaceae	11
Arctostaphylos	Ericaceae	9
Hesperolinon	Linaceae	9
Carex	Cyperaceae	7
Lomatium	Apiaceae	7
Erythranthe	Phrymaceae	6
Navarretia	Polemoniaceae	6
Packera	Asteraceae	6
Phacelia	Boraginaceae	6
Sedum	Crassulaceae	6
Calystegia	Convolvulaceae	5
Campanula	Campanulaceae	5
Cordylanthus	Orobanchaceae	5
Erigeron	Asteraceae	5
Fritillaria	Liliaceae	5
Monardella	Lamiaceae	5
Boechera	Brassicaceae	4
Calochortus	Liliaceae	4
Castilleja	Orobanchaceae	4
Ceanothus	Rhamnaceae	4
Cirsium	Asteraceae	4
Galium	Rubiaceae	4
Harmonia	Asteraceae	4
Horkelia	Rosaceae	4
Lessingia	Asteraceae	4

Brassicaceae, Apiaceae, Caryophyllaceae, and Liliaceae. Genera that follow the same pattern of notable enrichment in serpentine endemics include *Streptanthus*, *Minuartia*, *Cordylanthus*, *Packera*, and *Hesperolinon*.

Of the five geographic regions identified by Safford et al. (2005), the North Coast region remains the geographic leader in number of serpentine endemic taxa (127), and the Klamath region supports the most serpentine endemics that are restricted to a

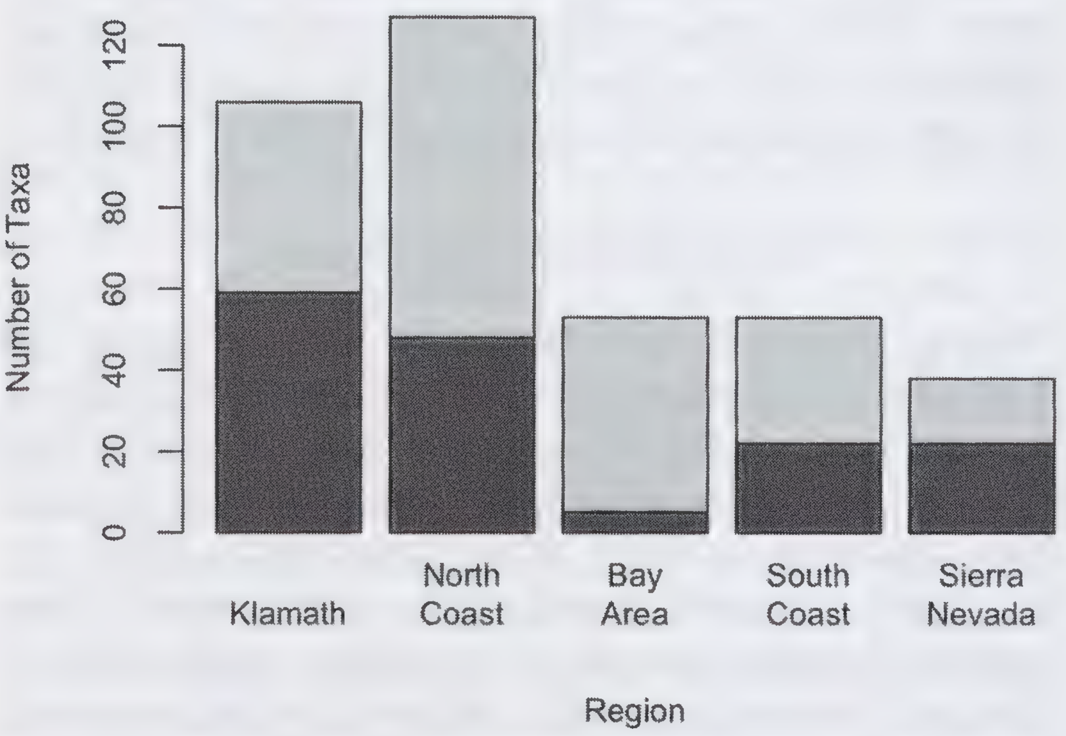

FIG. 1. Geographic distribution of serpentine endemic taxa (mean score ≥ 4.5) in California. Dark areas of bars represent taxa restricted to a single geographic region, and light areas represents taxa that also occur in other regions. Geographic regions are from Baldwin et al. (2012).

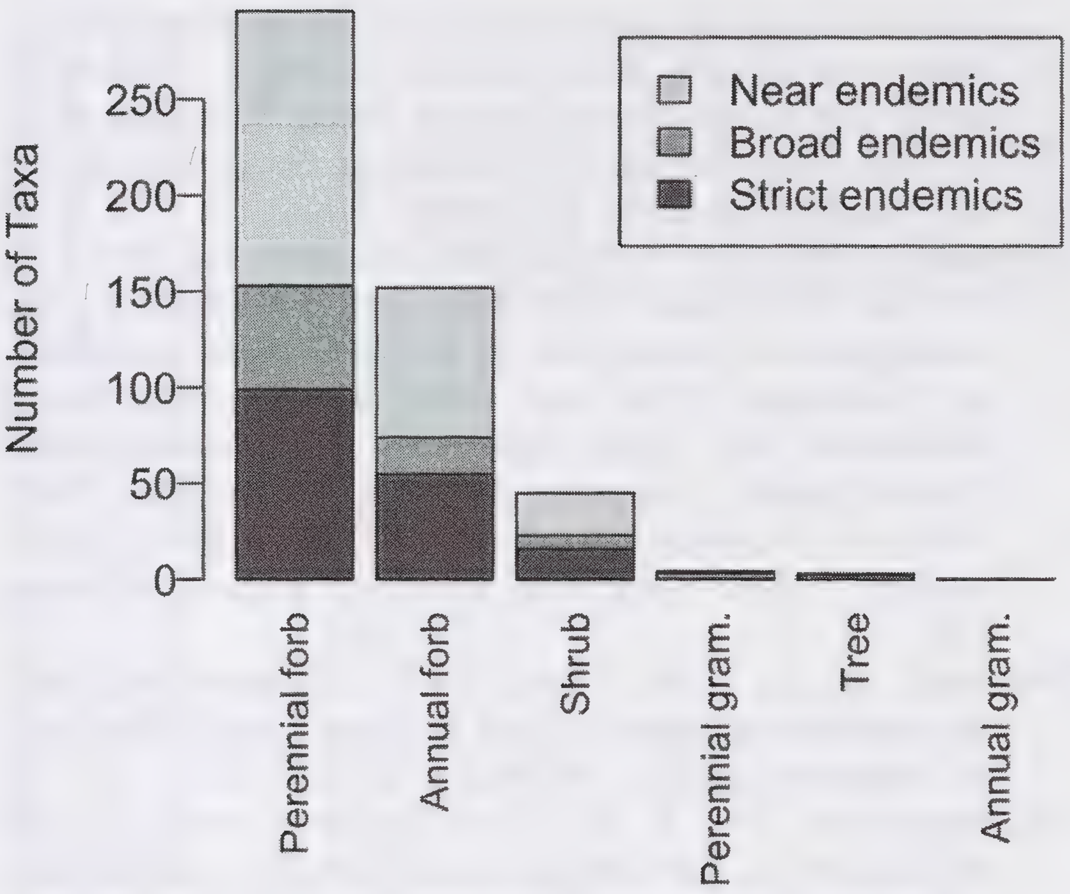

FIG. 2. Lifeforms of serpentine endemic and near endemic taxa (mean score >= 3.5) in California.

single region (60; Fig. 1). Together, the North Coast and Klamath regions support 146 serpentine endemic taxa that are found nowhere else in the state. See Safford (2011) for a figure and short discussion regarding the elevational distribution of serpentine endemic taxa in California. In short, most taxa grow in habitats below 1000 m elevation and few are found above 1500 m, primarily due to the relative rarity of ultramafic outcrops above that elevation.

Among the endemic taxa, 216 are dicots, 35 are monocots, two are gymnosperms, and two are pteridophytes (Appendix 1). The distribution of life forms is shown in Fig. 2. Serpentine endemic taxa in California are primarily perennial forbs (153 of 255 taxa, including three that can also be annuals), most of the rest are annual forbs (74 taxa, including the same three taxa); less than 10% of the endemic taxa in our database are woody species (Fig. 2).

192 (77%) of the endemic taxa in our database are listed in the CNPS Inventory of Rare and Endangered Plants (CNPS 2019). 108 serpentine endemic taxa are assigned California Rare Plant Rank 1B, which includes Federal and State threatened and endangered taxa as well as those taxa that the California Native Plant Society believes warrant listing (Appendix 1).

The richness of serpentine endemic taxa in California is astonishing, given the limited area of the state that supports ultramafic rocks and soils. Yet, amazingly, new species continue to be described from ultramafic soils in California. Only 15 years after embarking on this exercise for the first time, we expanded the list of California serpentine endemics by 3.7%. Given the outsized contribution made to California's natural riches by ultramafic substrates and their biota, we hope and expect that botanical and geoecological exploration will continue to expand the California serpentine flora, as well as our understanding of the factors that make it so diverse.

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LITERATURE CITED

ALEXANDER, E. B., R. G. COLEMAN, T. KEELER-WOLF, AND S. HARRISON. 2007. Serpentine geoecology of western North America. Oxford University Press, New York, NY.

ANACKER, B. L., W. JUSTEN, E. E. GOLDBERG, AND S. P. HARRISON. 2010. Origins and consequences of serpentine endemism in the California Flora. Evolution 65:365–376.

BALDWIN, B. G., D. H. GOLDMAN, D. J. KEIL, R. PATTERSON, T. J. ROSATTI, AND D. H. WILKEN (eds.). 2012. The Jepson manual: vascular plants of California. 2nd edition. University of California Press, Berkeley, CA.

BROOKS, R. R. 1987. Serpentine and its vegetation. Dioscorides Press, Portland, OR.

BRUMMITT, R. K., AND S. NAMOFF. 2013. *Calystegia vanzuukiae* (Convolvulaceae), a remarkable new species from central California. Aliso 31:15–18.

BURGE, D. O., J. H. THORNE, S. P. HARRISON, L. HARDISON, B. O'BRIEN. 2016. Plant diversity and endemism in the California Floristic Province. Madroño 63:3–216.

THE CALFLORA DATABASE. 2019. CalFlora: Information on California plants for education, research and conservation. Website: https://www.calflora.org/ [Accessed: 18 November, 2019].

CALIFORNIA NATIVE PLANT SOCIETY, RARE PLANT PROGRAM. 2020. Inventory of Rare and Endangered Plants of California (online edition, v8-03 0.39). Website: http://www.rareplants.cnps.org [accessed 18 November, 20219].

CCH1. 2019. Consortium of California Herbaria, CCH1 Portal. Website: http://ucjeps.berkeley.edu/consortium/ [accessed on 19 November 2019].

CCH2. 2019. Consortium of California Herbaria, CCH2 Portal. Website: http://cch2.org/portal/index.php [accessed on 19 November 2019].

ECKERT, A. J. 2006. Influence of Substrate Type and Microsite Availability on the Persistence of Foxtail Pine (Pinus balfouriana, Pinaceae) in the Klamath Mountains, California. American Journal of Botany 93:1615–1624.

HARRISON, S., AND N. RAJAKARUNA (eds.). 2011. Serpentine: the evolution and ecology of a model system. University of California Press, Berkeley, CA.

HARRISON, S. P., J. H. VIERS, AND J. F. QUINN. 2000. Climatic and spatial patterns of diversity in the serpentine plants of California. Diversity and Distributions 6:153–161.

Harrison, S. P., H. D. Safford, J. Grace, J. H. Viers, and K. F. Davies. 2006. Regional and local species richness in an insular environment: serpentine plants in California. Ecological Monographs 76:41–56.

Jepson Flora Project (eds.). 2019. Jepson eFlora, http://ucjeps.berkeley.edu/eflora/ [accessed on 10 January 2019].

Kofron, C.P., C. Rutherford, E.R. Clark, D. Woodbury, J. Olson, and R.F. Holland. 2013. Review of the purple amole *Chlorogalum purpureum* (Agavaceae): a threatened plant in the coast ranges of Central California. Bulletin, Southern California Academy of Sciences 112:38–48.

Nesom, G. L. 2017. Taxonomic review of the *Erythranthe moschata* complex (Phrymaceae). Phytoneuron 2017-17:1–29.

O'Donnell, R. 2006. A new species of *Hesperolinon* (Linaceae) from hunting creek in Napa County, California. Madroño 53:404–408.

Preston, R. E. 2006. A reconsideration of *Brodiaea minor* (Benth.) S. Watson and *Brodiaea purdyi* Eastwood (Themidaceae), with the resurrection of *Brodiaea nana* Hoover. Madroño 1:46–54.

Preston, R. E. 2013. A revision of *Brodiaea coronaria* (Asparagaceae: Brodiaeoideae): morphometric analysis and recognition of new and emended taxa. Systematic Botany 38:1012–1028.

Safford, H. D. 2011. Serpentine endemism in the California flora. Fremontia 39:32–39.

Safford, H. D., and S. P. Harrison. 2004. The effects of fire and grazing on serpentine versus non-serpentine grassland and chaparral. Pp. 315–322 *in* Boyd, R. S., Baker, A. J. M., and Proctor, J. (eds.), Ultramafic rocks: their soils, vegetation and fauna. Proceedings of the 4th International Conference on Serpentine Ecology. Science Reviews, St. Albans, UK.

Safford, H. D., and S. P. Harrison. 2008. The effects of fire on serpentine vegetation and implications for management. Proceedings of the 2002 Fire Conference on Managing Fire and Fuels in the Remaining Wildlands and Open Spaces of the Southwestern United States. December 2–5, 2002, San Diego, CA. General Technical Report PSW-189. USDA-Forest Service, Pacific Southwest Research Station, Albany, CA.

Safford, H. D., J. H. Viers, and S. Harrison. 2005. Serpentine endemism in the California flora: a database of serpentine affinity. Madroño 52: 222–257.

Southworth, D., L. E. Tackaberry, and H. B. Massicotte. 2014. Mycorrhizal ecology on serpentine soils. Plant Ecology & Diversity 7:445–455.

Stoughton, A. T. R., D. D. Jolles, and R. L. O. Quinn. 2017. The western spring beauties , *Claytonia lanceolata* (Montiaceae): a review and revised taxonomy for California. Systematic Botany 42:283–300.

Wilson, B., R. E. Brainerd, and N. J. Otting. 2014. *Sedum kiersteadiae* (Crassulaceae), a newly described species from the Klamath region of California, U.S.A. Journal of the Botanical Research Institute of Texas 8:9–15.

Zika, P. F., B. L. Wilson, R. E. Brainerd, and N. Otting. 2018. A review of *Sedum* section Gormania (Crassulaceae) in western North America. Phytotaxa 368:1–61.

APPENDIX 1. Updated list of taxa associated with serpentine ordered by family and taxon.[1] Names as in the Jepson eFlora (except for species listed in Table 2); [2] Aff = Affinity: SE = strict endemic, BE = broad endemic, BE/SI = broad endemic/strong indicator, SI = strong indicator, WI = weak indicator, WI/IN = weak indicator/indifferent. [3] Mean affinity score. [4] Sum of all affinity scores. [5] Median of affinity scores. [6] Standard deviation of affinity scores. [7] California Native Plant Society rarity codes (CNPS 2019). [8] Geographic distribution: KL = Klamath Ranges, NC = North Coast Ranges, BA = San Francisco Bay Area, SC = South Coast Ranges, SN = Sierra Nevada. [9] Life forms are abbreviated as follows: carn = carnivorous, cesp = cespitose, hemipar = hemiparasitic, paras = parasitic, rhiz = rhizomatous.

										Geog. Distribution[8]					
Taxon[1]	Authority	Family	Aff[2]	Mean[3]	Sum[4]	Sourc.	Med[5]	SD[6]	Rarity[7]	KL	NC	BA	SC	SN	Lifeform[9]
Chlorogalum angustifolium	Kellogg	Agavaceae	WI	2.4	9.5	4	1.8	2.8			1			1	Perennial forb (bulb)
Chlorogalum grandiflorum	Hoover	Agavaceae	WI/IN	1	2	2	1	-	1B.2					1	Perennial forb (bulb)
Chlorogalum pomeridianum var. *minus*	(DC.) Kunth	Agavaceae	SE	6	30	5	6	0	1B.2		1	1	1		Perennial forb (bulb)
Hastingsia alba	(Durand) S. Watson	Agavaceae	SI	3.4	17	5	3	1.5		1	1			1	Perennial forb (bulb)
Hastingsia serpentinicola	R. Becking	Agavaceae	SE	6	18	3	6	0		1	1				Perennial forb (bulb)
Allium acuminatum	Hook.	Alliaceae	WI	1.5	4.5	3	2	0.9		1	1	1			Perennial forb (bulb)
Allium amplectens	Torr.	Alliaceae	WI	2.3	11.3	5	2	2.2		1	1	1	1	1	Perennial forb (bulb)
Allium bolanderi var. *bolanderi*	S. Watson	Alliaceae	WI/IN	1.1	4.5	4	1	0.6		1	1	1			Perennial forb (bulb)
Allium bolanderi var. *mirabile*	S. Watson	Alliaceae	WI	2	4	2	2	-		1	1				Perennial forb (bulb)
Allium cratericola	Eastw.	Alliaceae	SI	2.6	15.8	6	2.5	1.9	CBR	1	1			1	Perennial forb (bulb)
Allium crispum	Greene	Alliaceae	WI/IN	1.3	3.75	3	1	0.7				1	1		Perennial forb (bulb)
Allium diabolense	(Ownbey & Aase ex Traub) McNeal	Alliaceae	SE	6	18	3	6	0					1		Perennial forb (bulb)
Allium falcifolium	Hook. & Arn.	Alliaceae	BE/SI	4.2	38	9	4	1.6		1	1	1			Perennial forb (bulb)
Allium fimbriatum var. *purdyi*	S. Watson	Alliaceae	BE	5.4	21.5	4	6	1.5	4.3		1				Perennial forb (bulb)
Allium hoffmanii	Ownbey ex Traub	Alliaceae	SE	6	30	5	6	0	4.3	1	1				Perennial forb (bulb)
Allium howellii var. *sanbenitense*	Eastw.	Alliaceae	BE/SI	4	12	3	4	1	1B.3				1		Perennial forb (bulb)
Allium jepsonii	(Ownbey & Aase ex Traub) S.S. Denison & McNeal	Alliaceae	BE	5.4	37.5	7	6	1	1B.2					1	Perennial forb (bulb)
Allium lacunosum var. *lacunosum*	S. Watson	Alliaceae	BE/SI	3.8	15.3	4	4.5	2.8				1	1		Perennial forb (bulb)
Allium lacunosum var. *micranthum*	S. Watson	Alliaceae	BE/SI	4.3	13	3	6	2.9	CBR				1		Perennial forb (bulb)
Allium membranaceum	Ownbey ex Traub	Alliaceae	WI/IN	1.3	4	3	1	1.5	CBR	1				1	Perennial forb (bulb)
Allium obtusum var. *conspicuum*	Lemmon	Alliaceae	WI/IN	1	2	2	1	-						1	Perennial forb (bulb)
Allium peninsulare var. *franciscanum*	Lemmon ex Greene	Alliaceae	WI	1.8	3.5	2	1.8	-	1B.2			1	1		Perennial forb (bulb)
Allium sanbornii var. *congdonii*	Alph. Wood	Alliaceae	SE	5.6	22.5	4	6	1	4.3					1	Perennial forb (bulb)
Allium sanbornii var. *sanbornii*	Alph. Wood	Alliaceae	SI	3.4	27	8	3.5	2.2	4.2					1	Perennial forb (bulb)
Allium serra	McNeal & Ownbey	Alliaceae	SI	2.6	10	4	3	1.5			1	1	1		Perennial forb (bulb)
Allium sharsmithiae	(Ownbey & Aase ex Traub) McNeal	Alliaceae	BE	5.1	20.5	4	6	2	1B.3			1	1		Perennial forb (bulb)
Allium siskiyouense	Ownbey ex Traub	Alliaceae	SI	2.8	14	5	2	1.8	4.3	1	1				Perennial forb (bulb)
Allium tuolumnense	(Ownbey & Aase ex Traub) S.S. Denison & McNeal	Alliaceae	SE	6	18	3	6	0	1B.2					1	Perennial forb (bulb)
Allium unifolium	Kellogg	Alliaceae	WI/IN	1	3	3	1	1			1	1	1		Perennial forb (bulb)
Angelica tomentosa	S. Watson	Apiaceae	SI	2.7	8	3	3	1.5		1	1		1		Perennial forb
Apiastrum angustifolium	Nutt.	Apiaceae	WI	1.5	7.6	5	0.1	2.5		1	1	1	1		Annual forb
Ligusticum californicum	J. M. Coult. & Rose	Apiaceae	WI/IN	1.4	5.75	4	1.4	1.3		1	1			1	Perennial forb
Lomatium ciliolatum	Jeps.	Apiaceae	SE	6	18	3	6	0			1	1	1		Perennial forb
Lomatium congdonii	J. M. Coult. & Rose	Apiaceae	SE	6	18	3	6	0	1B.2					1	Perennial forb
Lomatium dasycarpum ssp. *dasycarpum*	(Torr. & A. Gray) J. M. Coult. & Rose	Apiaceae	BE/SI	3.6	21.5	6	3.5	1.9			1	1	1		Perennial forb
Lomatium engelmannii	Mathias	Apiaceae	SE	5.8	34.5	6	6	0.8	4.3	1	1				Perennial forb
Lomatium hooveri	(Mathias & Constance) Constance & Ertter	Apiaceae	SE	5.9	29.5	5	6	0.4	4.3		1				Perennial forb
Lomatium howellii	(S. Watson) Jeps.	Apiaceae	SE	6	24	4	6	0	4.3	1					Perennial forb
Lomatium macrocarpum	(Torr. & A. Gray) J. M. Coult. & Rose	Apiaceae	SI	2.7	8	3	3	0.6		1	1	1	1	1	Perennial forb
Lomatium marginatum var. *marginatum*	(Benth.) J. M. Coult. & Rose	Apiaceae	WI	2.3	9	4	2.5	2.1		1	1			1	Perennial forb

APPENDIX 1. CONTINUED.

Taxon[1]	Authority	Family	Aff[2]	Mean[3]	Sum[4]	Sourc.	Med[5]	SD[6]	Rarity[7]	Geog. Distribution[8]					Lifeform[9]
										KL	NC	BA	SC	SN	
Lomatium marginatum var. *purpureum*	(Benth.) J. M. Coult. & Rose	Apiaceae	SI	3.3	13	4	3	2.2	CBR		1			1	Perennial forb
Lomatium observatorium	Constance & Ertter	Apiaceae	WI/IN	1.4	2.75	2	1.4	-	1B.2			1	1		Perennial forb
Lomatium parvifolium	(Hook. & Arn.) Jeps.	Apiaceae	SI	3.3	13	4	3	2.3	4.2				1		Perennial forb
Lomatium repostum	(Jeps.) Mathias	Apiaceae	SI	3.2	12.6	4	3	2.4	4.3		1				Perennial forb
Lomatium tracyi	Mathias & Constance	Apiaceae	SE	6	42	7	6	0	4.3	1	1				Perennial forb
Lomatium triternatum var. *triternatum*	(Pursh) J. M. Coult. & Rose	Apiaceae	SI	2.8	11	4	2	2.4		1	1				Perennial forb
Lomatium utriculatum	(Nutt. ex Torr. & A. Gray) J. M. Coult. & Rose	Apiaceae	WI	1.7	8.5	5	1	1.4		1	1	1	1	1	Perennial forb
Perideridia bacigalupii	Chuang & Constance	Apiaceae	BE	4.6	23	5	6	2.4	4.2					1	Perennial forb
Perideridia kelloggii	(A. Gray) Mathias	Apiaceae	WI	2.1	10.6	5	2	2			1	1	1	1	Perennial forb
Perideridia leptocarpa	T. I. Chuang & Constance	Apiaceae	SE	5.6	22.5	4	6	1	4.3	1					Perennial forb
Perideridia oregana	(S. Watson) Mathias	Apiaceae	WI	1.7	5	3	1	1.2		1	1	1	1		Perennial forb
Perideridia pringlei	(J. M. Coult. & Rose) A. Nelson & J. F. Macbr.	Apiaceae	BE/SI	3.7	18.5	5	3	2.3	4.3				1		Perennial forb
Sanicula bipinnatifida	Hook.	Apiaceae	WI	1.8	7.1	4	2	1.5		1	1	1	1	1	Perennial forb
Sanicula hoffmannii	(Munz) R. H. Shan & Constance	Apiaceae	WI	1.8	3.5	2	1.5	-	4.3				1		Perennial forb
Sanicula maritima	S. Watson	Apiaceae	WI	2.3	4.5	2	2	-	1B.1			1	1		Perennial forb
Sanicula peckiana	J. F. Macbr.	Apiaceae	BE	5.3	26.5	5	6	1.3	4.3	1					Perennial forb
Sanicula tracyi	R. H. Shan & Constance	Apiaceae	WI	2.1	8.5	4	1	2.6	4.2		1				Perennial forb
Sanicula tuberosa	Torr.	Apiaceae	WI/IN	1.3	3.75	3	1	0.7			1		1	1	Perennial forb
Tauschia glauca	(J. M. Coult. & Rose) Mathias & Constance	Apiaceae	BE/SI	3.5	10.5	3	3	0.6	4.3		1				Perennial forb
Tauschia hartwegii	(A. Gray) J. F. Macbr.	Apiaceae	WI/IN	1.3	4	3	1	1.5				1	1	1	Perennial forb
Tauschia howellii	(J. M. Coult. & Rose) J. F. Macbr.	Apiaceae	WI	2.3	7	3	1	3.2	1B.3	1					Perennial forb
Tauschia kelloggii	(A. Gray) J. F. Macbr.	Apiaceae	SI	2.6	12.8	5	2	2.2			1		1	1	Perennial forb
Asclepias solanoana	Woodson	Apocynaceae	SE	6	42	7	6	0	4.2		1				Perennial forb
Agoseris heterophylla	(Nutt.) Greene	Asteraceae	WI/IN	1.4	4.1	3	1	1.5		1	1	1	1	1	Annual forb
Ancistrocarphus filagineus	A. Gray	Asteraceae	SI	3.3	13	4	3	0.5		1	1	1	1	1	Annual forb
Antennaria argentea	Benth.	Asteraceae	WI	1.9	7.75	4	0.8	2.7		1	1				Perennial forb
Antennaria sawyeri	R.J. Bayer & Figura	Asteraceae	SE	6	18	3	6	0	1B.2	1					Perennial forb
Antennaria suffrutescens	Greene	Asteraceae	SE	5.6	22.5	4	6	1	4.3	1	1				Perennial forb
Arnica cernua	Howell	Asteraceae	SE	6	24	4	6	0	4.3	1					Perennial forb (rhiz.)
Arnica spathulata	Greene	Asteraceae	SE	5.5	16.5	3	6	1.2	4.3	1					Perennial forb (rhiz.)
Balsamorhiza macrolepis	W. M. Sharp	Asteraceae	SI	2.5	15	6	2	1.1	1B.2			1		1	Perennial forb
Balsamorhiza sericea	W.A. Weber	Asteraceae	SE	6	18	3	6	0	1B.3	1					Perennial forb
Benitoa occidentalis	(H. M. Hall) D. D. Keck	Asteraceae	BE/SI	4.1	16.5	4	4	1.8	4.3				1		Annual forb
Brickellia greenei	A. Gray	Asteraceae	BE/SI	3.7	11	3	4	0.6		1	1			1	Perennial forb
Cacaliopsis nardosmia	(A. Gray) A. Gray	Asteraceae	WI/IN	1.3	4	3	2	1.2		1	1				Perennial forb
Calycadenia multiglandulosa	DC.	Asteraceae	SI	3.1	15.5	5	3	1.2			1	1	1	1	Annual forb
Calycadenia oppositifolia	(Greene) Greene	Asteraceae	SI	2.6	18	7	2	1.6	4.2					1	Annual forb
Calycadenia pauciflora	A. Gray	Asteraceae	BE	5.3	21	4	5.5	1			1				Annual forb
Calycadenia truncata	DC.	Asteraceae	WI	2.1	12.5	6	2.5	1.1		1	1	1	1	1	Annual forb
Chaenactis glabriuscula var. *glabriuscula*	DC.	Asteraceae	WI	1.7	5.1	3	2	1.5				1	1	1	Perennial forb
Chaenactis glabriuscula var. *heterocarpha*	DC.	Asteraceae	SI	2.5	10	4	2.5	0.6			1	1	1	1	Annual forb
Chaenactis suffrutescens	A. Gray	Asteraceae	SE	6	30	5	6	0	1B.3	1					Perennial forb
Cirsium andrewsii	(A. Gray) Jeps.	Asteraceae	WI	1.7	5	3	2	0.9	1B.2			1			Perennial forb
Cirsium cymosum	(Greene) J. T. Howell	Asteraceae	SI	3	12	4	2	2		1	1	1	1	1	Perennial forb
Cirsium douglasii var. *breweri*	DC.	Asteraceae	SI	3	12	4	3	1.6		1	1			1	Perennial forb
Cirsium fontinale var. *campylon*	(Greene) Jeps.	Asteraceae	SE	5.9	29.5	5	6	0.4	1B.2			1	1		Perennial forb
Cirsium fontinale var. *fontinale*	(Greene) Jeps.	Asteraceae	SE	6	30	5	6	0	1B.1			1	1		Perennial forb

APPENDIX 1. CONTINUED.

Taxon[1]	Authority	Family	Aff[2]	Mean[3]	Sum[4]	Sourc.	Med[5]	SD[6]	Rarity[7]	Geog. Distribution[8]					Lifeform[9]
										KL	NC	BA	SC	SN	
Cirsium fontinale var. *obispoense*	(Greene) Jeps.	Asteraceae	SE	6	24	4	6	0	1B.2				1		Perennial forb
Cirsium hydrophilum var. *vaseyi*	(Greene) Jeps.	Asteraceae	SE	6	24	4	6	0	1B.2		1	1			Perennial forb
Cirsium remotifolium	(Hook.) DC.	Asteraceae	WI/IN	1	3.1	3	1	1		1	1	1			Perennial forb
Corethrogyne filaginifolia	(Hook. & Arn.) Nutt.	Asteraceae	WI/IN	1.3	4	3	1	1.5		1	1	1	1	1	Perennial forb, Shrub
Crepis pleurocarpa	A. Gray	Asteraceae	WI	2	10	5	2	0.7		1	1			1	Perennial forb
Deinandra halliana	(D. D. Keck) B. G. Baldwin	Asteraceae	SI	3	12	4	3	2.4	1B.2				1		Annual forb
Ericameria arborescens	(A. Gray) Greene	Asteraceae	WI/IN	1.3	4	3	1	1.5		1	1		1	1	Shrub
Ericameria greenei	(A. Gray) G. L. Nesom	Asteraceae	WI	2	8.1	4	1.5	2.1		1	1			1	Shrub
Ericameria nauseosa var. *oreophila*	(Pall. ex Pursh) G. L. Nesom & G. I. Baird	Asteraceae	WI	1.8	8.85	5	2	1.5		1	1			1	Shrub
Ericameria ophitidis	(J. T. Howell) G. L. Nesom	Asteraceae	SE	5.5	38.5	7	6	1	4.3	1	1				Shrub
Erigeron bloomeri var. *nudatus*	A. Gray	Asteraceae	SE	6	18	3	6	0	2B.3	1					Perennial forb
Erigeron cervinus	Greene	Asteraceae	SI	3.3	10	3	4	3.1	4.3	1					Perennial forb (rhiz.)
Erigeron foliosus var. *confinis*	Nutt.	Asteraceae	BE/SI	3.7	11	3	3	1.2		1					Perennial forb
Erigeron greenei	G. L. Nesom	Asteraceae	BE	4.8	24	5	4	1.1	1B.2		1				Perennial forb
Erigeron lassenianus var. *deficiens*	Greene	Asteraceae	WI	1.7	5	3	2	1.5	1B.3					1	Perennial forb
Erigeron petrophilus var. *sierrensis*	Greene	Asteraceae	BE	4.8	28.5	6	6	2.1	4.3					1	Perennial forb (rhiz.)
Erigeron petrophilus var. *viscidulus*	Greene	Asteraceae	WI	2.4	9.5	4	2	0.5	4.3	1					Perennial forb (rhiz.)
Erigeron reductus	(Cronquist) G. L. Nesom	Asteraceae	WI	2	8	4	2	1.6		1	1			1	Perennial forb
Erigeron robustior	(Cronquist) G. L. Nesom	Asteraceae	WI	1.5	4.5	3	2	1.2	4.3		1				Perennial forb
Erigeron serpentinus	G. L. Nesom	Asteraceae	SE	6	18	3	6	0	1B.3		1				Perennial forb
Eriophyllum confertiflorum var. *tanacetiflorum*	(DC.) A. Gray	Asteraceae	WI	1.9	3.75	2	1.9	-	4.3					1	Shrub
Eriophyllum jepsonii	Greene	Asteraceae	BE/SI	3.5	17.5	5	3	1.5	4.3			1	1		Shrub
Eriophyllum lanatum var. *achilleoides*	(Pursh) J. Forbes	Asteraceae	WI	2.3	7	3	2	0.6		1	1	1	1	1	Shrub
Eriophyllum lanatum var. *lanceolatum*	(Pursh) J. Forbes	Asteraceae	WI	1.7	5	3	2	1.5		1	1				Shrub
Eriophyllum latilobum	Rydb.	Asteraceae	SE	5.5	16.5	3	6	1.2	1B.1			1	1		Shrub
Grindelia camporum	Greene	Asteraceae	WI	1.8	5.25	3	2	1.4			1			1	Perennial forb
Grindelia hirsutula	Hook. & Arn.	Asteraceae	WI/IN	1.4	8.3	6	1	1				1	1		Perennial forb
Gutierrezia californica	(DC.) Torr. & A. Gray	Asteraceae	WI	1.8	5.25	3	2	1.4	CBR		1	1	1		Perennial forb, Shrub
Harmonia doris-nilesiae	(T. W. Nelson & J. P. Nelson) B. G. Baldwin	Asteraceae	BE	5.4	32.5	6	5.5	0.8	1B.1	1					Annual forb
Harmonia guggolziorum	B. G. Baldwin	Asteraceae	SE	6	18	3	6	0	1B.1		1				Annual forb
Harmonia hallii	(D. D. Keck) B. G. Baldwin	Asteraceae	SE	6	24	4	6	0	1B.2		1				Annual forb
Harmonia stebbinsii	(T. W. Nelson & J. P. Nelson) B. G. Baldwin	Asteraceae	SE	6	42	7	6	0	1B.2		1				Annual forb
Hazardia stenolepis	(H. M. Hall) Hoover	Asteraceae	WI	2	6.1	3	3	1.7	CBR				1		Shrub (stem succulent)
Hazardia whitneyi var. *discoidea*	(A. Gray) Greene	Asteraceae	WI	1.9	5.75	3	2	1.1		1					Perennial forb, Shrub
Hazardia whitneyi var. *whitneyi*	(A. Gray) Greene	Asteraceae	WI/IN	1	2	2	1	-						1	Perennial forb, shrub
Helenium bigelovii	A. Gray	Asteraceae	SI	2.9	11.5	4	2.5	2.3		1	1		1	1	Perennial forb
Helianthus exilis	A. Gray	Asteraceae	SE	5.7	45.5	8	6	1.1	4.2	1	1		1	1	Annual, Perennial forb
Hemizonia congesta ssp. *calyculata*	DC.	Asteraceae	WI	1.5	4.5	3	2	1.2	4.3		1				Annual forb
Hemizonia congesta ssp. *congesta*	DC.	Asteraceae	WI/IN	1.3	4	3	2	1.2	1B.2		1	1	1		Annual forb
Hemizonia congesta ssp. *tracyi*	DC.	Asteraceae	WI	1.8	5.25	3	2	0.7	4.3		1				Annual forb
Hesperevax sparsiflora var. *sparsiflora*	(A. Gray) Greene	Asteraceae	WI	1.8	7.25	4	1.5	1.6			1	1	1		Annual forb
Heterotheca oregona var. *oregona*	(Nutt.) Shinners	Asteraceae	WI	2	6	3	3	1.7		1	1		1		Perennial forb
Hieracium bolanderi	A. Gray	Asteraceae	BE/SI	3.8	15	4	4.5	2.6		1	1				Perennial forb
Hieracium greenei	A. Gray	Asteraceae	WI	2.2	6.5	3	3	1.4		1	1				Perennial forb
Lagophylla glandulosa	A. Gray	Asteraceae	WI	2	6.1	3	3	1.7			1			1	Annual forb
Lagophylla minor	(D. D. Keck) D. D. Keck	Asteraceae	BE	4.7	23.5	5	5	1.7	CBR		1			1	Annual forb

APPENDIX 1. CONTINUED.

Taxon[1]	Authority	Family	Aff[2]	Mean[3]	Sum[4]	Sourc.	Med[5]	SD[6]	Rarity[7]	Geog. Distribution[8]					Lifeform[9]
										KL	NC	BA	SC	SN	
Layia discoidea	D. D. Keck	Asteraceae	SE	5.7	28.5	5	6	0.8	1B.1				1		Annual forb
Layia jonesii	A. Gray	Asteraceae	BE/SI	3.5	10.5	3	3	0.6	1B.2				1		Annual forb
Layia septentrionalis	D. D. Keck	Asteraceae	SI	3.2	19	6	3.5	1.4	1B.2		1				Annual forb
Leptosyne stillmanii	A. Gray	Asteraceae	SI	2.7	8	3	3	0.6			1		1	1	Annual forb
Lessingia arachnoidea	Greene	Asteraceae	SE	6	18	3	6	0	1B.2			1			Annual forb
Lessingia hololeuca	Greene	Asteraceae	SI	2.5	7.5	3	3	1.2	3		1	1			Annual forb
Lessingia micradenia var. *glabrata*	Greene	Asteraceae	BE	5.1	30.5	6	5.5	1.3	1B.2			1			Annual forb
Lessingia micradenia var. *micradenia*	Greene	Asteraceae	BE	5.3	31.5	6	5.5	1	1B.2			1			Annual forb
Lessingia nemaclada	Greene	Asteraceae	WI	2	6	3	2	1		1	1	1	1	1	Annual forb
Lessingia ramulosa	A. Gray	Asteraceae	BE	5.4	27	5	6	1.3			1			1	Annual forb
Luina hypoleuca	Benth.	Asteraceae	WI/IN	1.4	4.25	3	2	1		1	1	1			Perennial forb
Madia exigua	(Sm.) A. Gray	Asteraceae	WI	1.8	7.25	4	2	1.4		1	1	1	1	1	Annual forb
Malacothrix clevelandii	A. Gray	Asteraceae	SI	3	9.1	3	3	3		1	1	1	1	1	Annual forb
Malacothrix floccifera	(DC.) S. F. Blake	Asteraceae	WI	2.1	6.25	3	3	1.6		1	1	1	1	1	Annual forb
Micropus amphibolus	A. Gray	Asteraceae	WI	2.4	7.25	3	1	3.1	3.2		1	1	1		Annual forb
Microseris douglasii	(DC.) Sch. Bip.	Asteraceae	WI/IN	1.3	4	3	1	0.6			1	1	1	1	Annual forb
Monolopia gracilens	A. Gray	Asteraceae	WI	2.4	4.75	2	2.4	-	1B.2			1	1		Annual forb
Packera clevelandii	(Greene) W. A. Weber & Á. Löve	Asteraceae	SE	5.8	46.5	8	6	0.7			1				Perennial forb
Packera eurycephala var. *eurycephala*	(Torr. & A. Gray) W.A. Weber & Á. Löve	Asteraceae	BE/SI	3.8	15	4	3	1.5		1	1				Perennial forb
Packera eurycephala var. *lewisrosei*	(Torr. & A. Gray) W.A. Weber & Á. Löve	Asteraceae	SE	5.8	40.5	7	6	0.8	1B.2					1	Perennial forb
Packera greenei	(A. Gray) W. A. Weber & Á. Löve	Asteraceae	BE	5.3	32	6	6	1.6		1	1				Perennial forb
Packera layneae	(Greene) W. A. Weber & Á. Löve	Asteraceae	BE	4.9	29.5	6	5	1.3						1	Perennial forb
Packera macounii	(Greene) W. A. Weber & Á. Löve	Asteraceae	BE	5.1	20.5	4	6	2	4.3	1					Perennial forb
Pentachaeta bellidiflora	Greene	Asteraceae	WI	2.4	7.25	3	3	1.3	1B.1			1			Annual forb
Pyrrocoma racemosa var. *congesta*	(Nutt.) Torr. & A. Gray	Asteraceae	SE	6	18	3	6	0	2B.3	1					Perennial forb
Pyrrocoma racemosa var. *pinetorum*	(Nutt.) Torr. & A. Gray	Asteraceae	BE/SI	4	16	4	4.5	2.4	4.2	1					Perennial forb
Pyrrocoma racemosa var. *racemosa*	(Nutt.) Torr. & A. Gray	Asteraceae	WI	1.7	5	3	1	2.1			1	1	1		Perennial forb
Raillardella pringlei	Greene	Asteraceae	SE	6	30	5	6	0	1B.2	1					Perennial forb
Rigiopappus leptocladus	A. Gray	Asteraceae	WI	1.9	7.5	4	2	1.3		1	1	1	1	1	Annual forb
Rudbeckia glaucescens	Eastw.	Asteraceae	BE	5.3	21	4	6	1.5		1	1				Perennial forb
Rudbeckia klamathensis	P. B. Cox & Urbatsch	Asteraceae	BE	5	10	2	5	-		1					Perennial forb
Sericocarpus oregonensis	Nutt.	Asteraceae	WI/IN	1.1	3.25	3	1	0.9		1	1			1	Perennial forb
Solidago guiradonis	A. Gray	Asteraceae	SE	6	18	3	6	0	4.3				1		Perennial forb
Solidago multiradiata	Aiton	Asteraceae	WI/IN	1.1	2.1	2	1.1	-		1				1	Perennial forb
Stebbinsoseris decipiens	(K. L. Chambers) K. L. Chambers	Asteraceae	WI	1.8	5.5	3	2	0.6	1B.2			1	1		Annual forb
Wyethia bolanderi	(A. Gray) W. A. Weber	Asteraceae	WI	1.5	3	2	1.5	-						1	Perennial forb
Berberis aquifolium var. *aquifolium*	Pursh	Berberidaceae	WI	1.6	4.75	3	1	1.2		1	1			1	Shrub
Berberis aquifolium var. *repens*	Pursh	Berberidaceae	WI	1.7	5	3	1	1.2		1	1			1	Shrub
Vancouveria chrysantha	Greene	Berberidaceae	SE	6	18	3	6	0	4.3	1	1				Perennial forb (rhiz.)
Vancouveria planipetala	Calloni	Berberidaceae	WI	1.7	5	3	1	1.2		1	1	1	1		Perennial forb (rhiz.)
Cryptantha dissita	I. M. Johnst.	Boraginaceae	BE/SI	4.4	17.5	4	4.5	2.1	1B.2		1				Annual forb
Cryptantha excavata	Brandegee	Boraginaceae	WI	1.5	3	2	1.5	-	1B.1		1				Annual forb
Cryptantha flaccida	(Lehm.) Greene	Boraginaceae	WI	1.6	4.75	3	2	0.7		1	1	1	1	1	Annual forb
Cryptantha hispidula	Brand	Boraginaceae	SE	6	24	4	6	0	CBR	1	1				Annual forb
Cryptantha intermedia var. *intermedia*	(A. Gray) Greene	Boraginaceae	WI/IN	1.4	4.1	3	1	1.5		1	1	1	1	1	Annual forb
Cryptantha mariposae	I. M. Johnst.	Boraginaceae	SE	6	18	3	6	0	1B.3					1	Annual forb
Cryptantha milobakeri	I.M. Johnston	Boraginaceae	SI	3.3	9.75	3	3	2.6		1	1			1	Annual forb
Emmenanthe penduliflora var. *penduliflora*	Benth.	Boraginaceae	WI	1.8	7	4	2	0.5			1	1	1	1	Annual forb

APPENDIX 1. CONTINUED.

Taxon[1]	Authority	Family	Aff[2]	Mean[3]	Sum[4]	Sourc.	Med[5]	SD[6]	Rarity[7]	Geog. Distribution[8] KL	NC	BA	SC	SN	Lifeform[9]
Emmenanthe penduliflora var. *rosea*	Benth.	Boraginaceae	BE/SI	4.3	17	4	4.5	1.7				1	1		Annual forb
Hackelia bella	(J. F. Macbr.) I. M. Johnst.	Boraginaceae	WI/IN	1.3	4	3	1	1.5	CBR	1	1				Perennial forb
Howellanthus dalesianus	(J.T.Howell) Walden & R.Patt.	Boraginaceae	SE	6	30	5	6	0	4.3	1					Perennial forb
Pectocarya pusilla	(A. DC.) A. Gray	Boraginaceae	WI/IN	1.3	2.5	2	1.3	-		1	1	1	1	1	Annual forb
Phacelia breweri	A. Gray	Boraginaceae	SE	5.5	11	2	5.5	-				1	1		Annual forb
Phacelia californica	Cham.	Boraginaceae	WI/IN	1.4	4.25	3	1	1.4			1	1	1		Perennial forb
Phacelia corymbosa	Jeps.	Boraginaceae	SE	5.5	33	6	6	0.8		1	1				Perennial forb
Phacelia distans	Benth.	Boraginaceae	WI/IN	1.1	2.1	2	1.1	-			1	1	1		Annual forb
Phacelia divaricata	(Benth.) A. Gray	Boraginaceae	WI	2.3	7	3	3	1.2			1	1	1		Annual forb
Phacelia egena	(Brand) J. T. Howell	Boraginaceae	WI	2.1	6.25	3	3	1.6		1	1	1	1	1	Perennial forb
Phacelia greenei	J. T. Howell	Boraginaceae	SE	6	36	6	6	0	1B.2	1					Annual forb
Phacelia imbricata var. *imbricata*	Greene	Boraginaceae	WI	1.7	5	3	1	1.2			1	1	1	1	Perennial forb
Phacelia leonis	J. T. Howell	Boraginaceae	BE/SI	3.9	27.5	7	4	1.1	1B.3	1					Annual forb
Phacelia phacelioides	(Benth.) Brand	Boraginaceae	BE/SI	4.2	12.5	3	6	3.2	1B.2			1	1		Annual forb
Phacelia pringlei	A. Gray	Boraginaceae	BE/SI	4	12	3	4	1	CBR	1					Annual forb
Phacelia purpusii	Brandegee	Boraginaceae	WI/IN	1.1	2.1	2	1.1	-						1	Annual forb
Arabis mcdonaldiana	Eastw.	Brassicaceae	BE	5.4	32.5	6	6	1	1B.1	1	1				Perennial forb
Arabis oregana	Rollins	Brassicaceae	BE/SI	3.8	11.5	3	3	2.1	4.3	1	1				Perennial forb
Boechera constancei	(Rollins) Al-Shehbaz	Brassicaceae	SE	5.9	41.5	7	6	0.4	1B.1					1	Perennial forb
Boechera koehleri	(Howell) Al-Shehbaz	Brassicaceae	BE	5.3	21	4	5.5	1	1B.3	1					Perennial forb
Boechera rollei	(Rollins) Al-Shehbaz	Brassicaceae	SE	6	12	2	6	-	1B.1	1					Perennial forb
Boechera serpenticola	Windham & Al-Shehbaz	Brassicaceae	BE	5.3	16	3	6	1.2	1B.2	1	1				Perennial forb
Boechera subpinnatifida	(S. Watson) Al-Shehbaz	Brassicaceae	WI	2.3	9	4	2.5	1		1	1				Perennial forb
Cardamine nuttallii	Greene	Brassicaceae	WI	2	2	1				1	1			1	Perennial forb (rhiz.)
Cardamine pachystigma var. *dissectifolia*	(S. Watson) Rollins	Brassicaceae	SE	5.5	60	11	6	0.9	1B.2		1			1	Perennial forb (rhiz.)
Caulanthus flavescens	(Hook.) Payson	Brassicaceae	WI	2.3	9.25	4	2.5	1.6			1	1	1		Annual forb
Draba aureola	S. Watson	Brassicaceae	SI	2.7	8	3	3	0.6	1B.3	1					Perennial forb
Draba carnosula	O. E. Schulz	Brassicaceae	SE	6	14	4	6	0	1B.3	1					Perennial forb
Draba howellii	S. Watson	Brassicaceae	WI/IN	1.4	4.25	3	1	1.4	4.3	1					Perennial forb
Erysimum franciscanum	Rossbach	Brassicaceae	SI	3	9	3	3	0	4.2		1	1	1		Perennial forb
Noccaea fendleri ssp. *californica*	(A. Gray) Holub	Brassicaceae	SE	6	30	5	6	0	1B.1		1				Perennial forb
Noccaea fendleri ssp. *glauca*	(A. Gray) Holub	Brassicaceae	BE/SI	4.4	22	5	4	1.5		1	1				Perennial forb
Streptanthus barbatus	S. Watson	Brassicaceae	SE	5.6	28	5	6	0.5	CBR	1					Perennial forb
Streptanthus barbiger	Greene	Brassicaceae	SE	6	24	4	6	0	4.2		1				Annual forb
Streptanthus batrachopus	J. L. Morrison	Brassicaceae	SE	6	24	4	6	0	1B.3		1	1			Annual forb
Streptanthus brachiatus	F. W. Hoffm.	Brassicaceae	SE	5.9	23.5	8	6	0.5			1				Annual, Perennial forb
Streptanthus breweri	A. Gray	Brassicaceae	SE	5.7	40	7	6	0.8		1	1	1	1		Annual forb
Streptanthus drepanoides	Kruckeb. & J. L. Morrison	Brassicaceae	SE	6	36	6	6	0	4.3	1	1			1	Annual forb
Streptanthus glandulosus ssp. *albidus*	Hook.	Brassicaceae	BE	5.3	31.5	6	6	1.3				1	1		Annual forb
Streptanthus glandulosus ssp. *glandulosus*	Hook.	Brassicaceae	BE/SI	3.7	40.3	11	3	1.7			1	1	1		Annual forb
Streptanthus glandulosus ssp. *hoffmanii*	Hook.	Brassicaceae	SI	3	3	1	3	-	1B.3		1				Annual forb
Streptanthus glandulosus ssp. *niger*	Hook.	Brassicaceae	SE	6	30	5	6	0	1B.1		1	1			Annual forb
Streptanthus glandulosus ssp. *pulchellus*	Hook.	Brassicaceae	BE	4.9	24.5	5	6	1.8			1	1			Annual forb
Streptanthus glandulosus ssp. *secundus*	Hook.	Brassicaceae	SI	3.3	20	6	3	1.5			1	1			Annual forb
Streptanthus glandulosus ssp. *sonomensis*	Hook.	Brassicaceae	SE	6	12	2	6	-			1				Annual forb
Streptanthus hesperidis	Jeps.	Brassicaceae	SE	6	24	4	6	0	1B.2		1				Annual forb
Streptanthus howellii	S. Watson	Brassicaceae	SE	6	30	5	6	0	1B.2	1					Perennial forb
Streptanthus insignis ssp. *insignis*	Jeps.	Brassicaceae	BE/SI	4	20	5	4	2.4					1		Annual forb
Streptanthus insignis ssp. *lyonii*	Jeps.	Brassicaceae	SI	3.3	16.5	5	2	2.7	1B.2				1		Annual forb
Streptanthus morrisonii	F. W. Hoffm.	Brassicaceae	SE	6	110	18	6	0	CBR		1				Annual, Perennial forb
Streptanthus polygaloides	A. Gray	Brassicaceae	SE	5.7	28.5	5	6	0.9						1	Annual forb
Streptanthus vernalis	R. O'Donnell & R. W. Dolan	Brassicaceae	SE	6	12	2	6	-	1B.2		1				Annual forb

APPENDIX 1. CONTINUED.

Taxon[1]	Authority	Family	Aff[2]	Mean[3]	Sum[4]	Sourc.	Med[5]	SD[6]	Rarity[7]	Geog. Distribution[8]					Lifeform[9]
										KL	NC	BA	SC	SN	
Streptanthus vimineus	(Greene) Al-Shehbaz & D.W. Taylor	Brassicaceae	SE	6	12	2	6	-			1				Annual forb
Thelypodium brachycarpum	Torr.	Brassicaceae	SI	3.3	10	3	3	0.6	4.2	1	1				Annual, Perennial forb
Campanula angustiflora	Eastw.	Campanulaceae	BE/SI	3.9	19.3	5	4	2.4			1	1			Annual forb
Campanula exigua	Rattan	Campanulaceae	BE/SI	3.9	19.5	5	4	1.5	1B.2			1	1		Annual forb
Campanula griffinii	Morin	Campanulaceae	SE	6	18	3	6	0	CBR		1	1	1		Annual forb
Campanula rotundifolia	L.	Campanulaceae	BE	5	15	3	6	1.7		1					Perennial forb
Campanula scabrella	Engelm.	Campanulaceae	SI	2.5	10	4	2.5	1.3	4.3	1					Perennial forb (rhiz.)
Campanula sharsmithiae	Morin	Campanulaceae	SE	6	18	3	6	0	1B.2			1	1		Annual forb
Campanula wilkinsiana	Greene	Campanulaceae	WI/IN	1	5	5	0	1.7	1B.2	1					Perennial forb (rhiz.)
Githopsis diffusa ssp. *candida*	A. Gray	Campanulaceae	WI/IN	1	2	2	1	-	CBR				1		Annual forb
Githopsis pulchella ssp. *campestris*	Vatke	Campanulaceae	WI	1.6	3.25	2	1.6	-						1	Annual forb
Githopsis pulchella ssp. *serpentinicola*	Vatke	Campanulaceae	BE	5.3	21	4	5.5	1	4.3					1	Annual forb
Githopsis pulchella var. *glabra*	Vatke	Campanulaceae	BE/SI	3.8	19	5	3	2						1	Annual forb
Githopsis pulchella var. *pulchella*	Vatke	Campanulaceae	WI/IN	1	1	1	1	-						1	Annual forb
Nemacladus montanus	Greene	Campanulaceae	SE	6	18	3	6	0	CBR		1	1	1		Annual forb
Cerastium arvense ssp. *strictum*	L.	Caryophyllaceae	WI	2.1	8.5	4	0.9	2.6		1	1	1	1	1	Perennial forb
Eremogone kingii var. *glabrescens*	(S. Watson) Ikonn.	Caryophyllaceae	WI/IN	1.4	4.1	3	2	1.1						1	Perennial forb
Minuartia californica	(A. Gray) Mattf.	Caryophyllaceae	WI	1.7	5	3	2	1.5		1	1	1	1	1	Annual forb
Minuartia cismontana	Meinke & Zika	Caryophyllaceae	WI	1.8	3.5	2	1.8	-		1	1	1	1	1	Annual, Perennial forb
Minuartia decumbens	T. W. Nelson & J. P. Nelson	Caryophyllaceae	SE	6	24	4	6	0		1	1				Perennial forb
Minuartia douglasii	(Fenzl ex Torr. & A. Gray) Mattf.	Caryophyllaceae	SI	3	15	5	3	0.7		1	1	1	1	1	Annual forb
Minuartia howellii	(S. Watson) Mattf.	Caryophyllaceae	SE	5.7	28.5	5	6	0.9		1					Perennial forb
Minuartia nuttallii var. *gregaria*	(Pax) Briq.	Caryophyllaceae	SI	3.2	16	5	3	1.9		1	1				Perennial forb
Minuartia rosei	(Maguire & Barneby) McNeill	Caryophyllaceae	SE	6	30	5	6	0		1	1				Perennial forb
Minuartia stolonifera	T. W. Nelson & J. P. Nelson	Caryophyllaceae	SE	6	30	5	6	0		1					Perennial forb
Moehringia macrophylla	(Hook.) Fenzl	Caryophyllaceae	SI	2.7	8	3	3	0.6		1	1	1	1	1	Perennial forb
Silene antirrhina	L.	Caryophyllaceae	WI/IN	1.1	3.25	3	1	0.9		1	1	1	1	1	Annual forb
Silene campanulata ssp. *campanulata*	S. Watson	Caryophyllaceae	BE	5.3	31.5	6	5.5	1	4.2	1	1				Perennial forb
Silene campanulata ssp. *glandulosa*	S. Watson	Caryophyllaceae	BE/SI	3.8	19	5	3	1.3		1	1				Perennial forb
Silene grayi	S. Watson	Caryophyllaceae	WI	1.8	5.5	3	2	1.3		1					Perennial forb
Silene hookeri	Nutt.	Caryophyllaceae	BE/SI	3.5	7	2	3.5	-		1	1				Perennial forb
Silene salmonacea	T. W. Nelson, J. P. Nelson, & S. A. Erwin	Caryophyllaceae	SI	3	6	2	3	-	1B.2	1					Perennial forb
Silene serpentinicola	T. W. Nelson & J. P. Nelson	Caryophyllaceae	SE	6	6	1	6	-		1					Perennial forb (rhiz.)
Crocanthemum scoparium	(Nutt.) Millsp.	Cistaceae	WI/IN	1	2	2	1	-						1	Shrub
Calystegia collina ssp. *collina*	(Greene) Brummitt	Convolvulaceae	BE	4.7	33	7	6	1.6			1	1			Perennial forb
Calystegia collina ssp. *oxyphylla*	(Greene) Brummitt	Convolvulaceae	SE	5.6	33.5	6	6	1.2	4.2		1				Perennial forb
Calystegia collina ssp. *tridactylosa*	(Greene) Brummitt	Convolvulaceae	BE	4.5	18	4	4.5	1.7	1B.2		1				Perennial forb
Calystegia collina ssp. *venusta*	(Greene) Brummitt	Convolvulaceae	BE	4.9	24.5	5	5	1.3	4.3				1		Perennial forb
Calystegia malacophylla	(Greene) Munz	Convolvulaceae	WI	1.5	4.5	3	1	1.3				1	1	1	Perennial forb
Calystegia vanzuukiae	Brummitt & Namoff	Convolvulaceae	BE	5	15	3	5	0	1B.3					1	Perennial forb
Convolvulus simulans	L. M. Perry	Convolvulaceae	BE/SI	3.7	14.8	4	4	2.4	4.2			1	1		Annual forb
Dudleya abramsii ssp. *bettinae*	Rose	Crassulaceae	SE	6	18	3	6	0	1B.2				1		Perennial forb
Dudleya abramsii ssp. *murina*	Rose	Crassulaceae	SE	6	18	3	6	0	1B.3				1		Perennial forb
Dudleya abramsii ssp. *setchellii*	Rose	Crassulaceae	SE	6	24	4	6	0	1B.1			1	1		Perennial forb
Dudleya blochmaniae ssp. *blochmaniae*	(Eastw.) Moran	Crassulaceae	SI	3.2	9.5	3	3	0	1B.1				1		Perennial forb
Sedella pentandra	H. Sharsm.	Crassulaceae	WI	2	8.1	4	1.5	2.1			1	1	1		Annual forb
Sedella pumila	(Benth.) Britton & Rose	Crassulaceae	WI	1.7	5.1	3	2	1.5			1			1	Annual forb
Sedum albomarginatum	R. T. Clausen	Crassulaceae	SE	5.9	47	8	6	0.4	1B.2					1	Perennial forb
Sedum citrinum	Zika	Crassulaceae	SE	6	18	3	6	0	1B.2	1					Perennial forb
Sedum eastwoodiae	(Britton) A. Berger	Crassulaceae	SE	6	30	5	6	0	1B.2		1				Perennial forb

APPENDIX 1. CONTINUED.

Taxon[1]	Authority	Family	Aff[2]	Mean[3]	Sum[4]	Sourc.	Med[5]	SD[6]	Rarity[7]	Geog. Distribution[8]					Lifeform[9]
										KL	NC	BA	SC	SN	
Sedum flavidum	B.L. Wilson & Zika	Crassulaceae	SI	3	18	6	3	0.6	4.3	1	1				Perennial forb
Sedum kiersteadiae	B.L. Wilson & R.E. Brainerd	Crassulaceae	SI	3.3	10	3	3	0.6	1B.2	1					Perennial forb
Sedum laxum ssp. *heckneri*	(Britton) A. Berger	Crassulaceae	SI	3.3	10	3	3	0.6	4.3	1	1				Perennial forb
Sedum laxum ssp. *laxum*	(Britton) A. Berger	Crassulaceae	BE	4.8	23	5	5	0.8		1	1				Perennial forb
Sedum patens	Zika	Crassulaceae	SE	6	6	1	6	-		1					Perennial forb
Sedum radiatum	S. Watson	Crassulaceae	WI	2	6	3	2	2		1	1	1	1	1	Annual forb
Sedum rubiginosum	Zika & B.L. Wilson	Crassulaceae	SE	6	6	1	6	-			1				Perennial forb
Calocedrus decurrens	(Torr.) Florin	Cupressaceae	SI	3	9	3	3	0		1	1	1	1	1	Tree
Chamaecyparis lawsoniana	(A. Murray bis) Parl.	Cupressaceae	SI	3	15	5	3	0.7	CBR	1	1				Tree
Hesperocyparis bakeri	(Jeps.) Bartel	Cupressaceae	SI	2.6	13	5	3	0.5	4.2	1				1	Tree
Hesperocyparis macnabiana	(A. Murray bis) Bartel	Cupressaceae	BE	4.7	28	6	4.5	1.2			1			1	Tree
Hesperocyparis sargentii	(Jeps.) Bartel	Cupressaceae	BE	4.9	34	7	5	1.2			1	1	1		Tree
Juniperus communis var. *jackii*	L.	Cupressaceae	BE/SI	4	8	2	4	-	CBR	1					Shrub
Calliscirpus criniger	(A. Gray) C.N. Gilmour, J.R. Starr, & Naczi	Cyperaceae	WI	1.7	5	3	1	2.1		1	1			1	Perennial gram.
Carex brainerdii	Mack.	Cyperaceae	WI/IN	1.4	4.25	3	2	1		1	1		1	1	Perennial gram. (rhiz.)
Carex concinnoides	Mack.	Cyperaceae	BE/SI	4	8	2	4	-		1	1				Perennial gram. (rhiz.)
Carex hirtissima	W. Boott	Cyperaceae	WI	1.8	3.5	2	1.8	-			1			1	Perennial gram. (cesp.)
Carex klamathensis	B.L. Wilson & Janeway	Cyperaceae	SE	6	12	2	6	-	1B.2	1	1				Perennial gram. (rhiz.)
Carex mendocinensis	Olney ex W. Boott	Cyperaceae	BE/SI	3.8	23	6	3.5	1.2		1	1			1	Perennial gram. (cesp.)
Carex obispoensis	Stacey	Cyperaceae	BE	4.9	24.5	5	6	1.6	1B.2				1		Perennial gram. (cesp.)
Carex scabriuscula	Mack.	Cyperaceae	SE	6	12	2	6	-	4.3	1				1	Perennial gram. (rhiz.)
Carex serpenticola	Zika	Cyperaceae	SE	5.5	11	2	5.5	-		1					Perennial gram. (rhiz.)
Carex serratodens	W. Boott	Cyperaceae	BE	4.9	39	8	5	1.1			1	1	1	1	Perennial gram. (cesp.)
Carex spissa	L. H. Bailey	Cyperaceae	SI	2.8	8.25	3	2	2.9					1		Perennial gram. (rhiz.)
Carex xerophila	Janeway & Zika	Cyperaceae	WI	1.7	5	3	2	0.6						1	Perennial gram. (cesp.)
Polystichum lemmonii	Underw.	Dryopteridaceae	SE	6	24	4	6	0		1	1			1	Perennial forb (rhiz.)
Polystichum scopulinum	(D. C. Eaton) Maxon	Dryopteridaceae	WI	1.7	5.1	3	2	1.5		1	1			1	Perennial forb (rhiz.)
Arctostaphylos bakeri ssp. *bakeri*	Eastw.	Ericaceae	SE	5.5	27.5	5	6	1.3	1B.1		1				Shrub
Arctostaphylos bakeri ssp. *sublaevis*	Eastw.	Ericaceae	SE	6	12	2	6	-	1B.2		1				Shrub
Arctostaphylos canescens ssp. *sonomensis*	Eastw.	Ericaceae	SI	2.5	12.5	5	3	1.5	CBR	1	1				Shrub
Arctostaphylos franciscana	Eastw.	Ericaceae	SE	6	18	3	6	0	1B.1			1	1		Shrub
Arctostaphylos hispidula	Howell	Ericaceae	BE	4.5	22.5	5	4	1.1	4.2	1	1				Shrub
Arctostaphylos klamathensis	S. W. Edwards, Keeler-Wolf & W. Knight	Ericaceae	BE/SI	3.9	19.5	5	4	1.8	1B.2	1					Shrub
Arctostaphylos montana ssp. *montana*	Eastw.	Ericaceae	BE	4.9	19.5	4	4.5	1	1B.3			1	1		Shrub
Arctostaphylos montana ssp. *ravenii*	Eastw.	Ericaceae	SE	6	18	3	6	0	1B.1			1	1		Shrub
Arctostaphylos nortensis	(P. V. Wells) P. V. Wells	Ericaceae	SI	2.8	5.5	2	2.5	-	4.3	1					Shrub
Arctostaphylos obispoensis	Eastw.	Ericaceae	SE	5.7	28.5	5	6	0.9	4.3				1		Shrub
Arctostaphylos stanfordiana ssp. *raichei*	Parry	Ericaceae	SI	2.6	10.5	4	3	1.7	1B.1		1				Shrub
Arctostaphylos viscida ssp. *pulchella*	Parry	Ericaceae	BE	5	25	5	5	1		1	1				Shrub
Arctostaphylos viscida ssp. *viscida*	Parry	Ericaceae	WI	2.2	10.8	5	3	1.2		1				1	Shrub
Pyrola dentata	Sm.	Ericaceae	WI	2	6	3	3	1.7		1	1				Perennial forb (rhiz.)
Vaccinium coccineum	Piper	Ericaceae	BE/SI	3.5	3.5	1	3	-	3.3	1					Shrub
Acmispon junceus var. *junceus*	(Benth.) Brouillet	Fabaceae	WI	1.5	3	2	1.5	-					1		Perennial forb
Astragalus breweri	A. Gray	Fabaceae	SI	3.2	15.8	5	3	2	4.2		1	1			Annual forb
Astragalus claranus	Jeps.	Fabaceae	SI	3	6	2	3	-			1				Annual forb
Astragalus clevelandii	Greene	Fabaceae	SE	6	24	4	6	0	4.3		1		1		Perennial forb
Astragalus curtipes	A. Gray	Fabaceae	WI	1.8	3.5	2	1.8	-	CBR				1		Perennial forb
Astragalus macrodon	(Hook. & Arn.) A. Gray	Fabaceae	WI/IN	1.3	3.75	3	1	0.7	4.3				1		Perennial forb
Astragalus rattanii var. *jepsonianus*	A. Gray	Fabaceae	BE/SI	4.3	25.5	6	4	1.2	1B.2		1				Annual forb
Astragalus whitneyi var. *siskiyouensis*	A. Gray	Fabaceae	BE	4.6	23	5	5	1.1		1	1				Perennial forb
Hoita strobilina	(Hook. & Arn.) Rydb.	Fabaceae	SI	2.5	5	2	2.5	-	1B.1			1			Perennial forb

APPENDIX 1. CONTINUED.

Taxon[1]	Authority	Family	Aff[2]	Mean[3]	Sum[4]	Sourc.	Med[5]	SD[6]	Rarity[7]	Geog. Distribution[8]					Lifeform[9]
										KL	NC	BA	SC	SN	
Lathyrus biflorus	T. W. Nelson & J. P. Nelson	Fabaceae	SE	6	24	4	6	0	1B.1		1				Perennial forb
Lathyrus delnorticus	C. L. Hitchc.	Fabaceae	BE	5.3	10.5	2	5	-	4.3	1					Perennial forb
Lathyrus vestitus var. *vestitus*	Nutt.	Fabaceae	WI	1.8	7.2	4	0.6	2.8			1	1	1		Perennial forb
Lupinus constancei	T. W. Nelson & J. P. Nelson	Fabaceae	SE	6	24	4	6	0	1B.1		1				Perennial forb
Lupinus croceus	Eastw.	Fabaceae	BE/SI	4	12	3	4	0		1					Perennial forb
Lupinus lapidicola	A. Heller	Fabaceae	SI	3	15	5	3	3		1	1				Perennial forb
Lupinus onustus	S. Watson	Fabaceae	SI	3.1	15.3	5	3	2.9		1				1	Perennial forb
Lupinus spectabilis	Hoover	Fabaceae	SE	6	24	4	6	0	1B.2					1	Annual forb
Pediomelum californicum	(S. Watson) Rydb.	Fabaceae	BE/SI	4.4	21.8	5	6	2.4			1	1	1		Perennial forb
Trifolium amoenum	Greene	Fabaceae	WI/IN	1.3	2.5	2	1	-	1B.1		1	1			Annual forb
Trifolium fucatum	Lindl.	Fabaceae	WI/IN	1.3	4	3	1	0.6			1		1		Annual forb
Trifolium gracilentum	Torr. & A. Gray	Fabaceae	WI/IN	1	3.1	3	1	1		1	1	1	1	1	Annual forb
Trifolium longipes ssp. *elmeri*	Nutt.	Fabaceae	BE	5.3	21	4	6	1.5		1	1				Perennial forb
Trifolium longipes ssp. *oreganum*	Nutt.	Fabaceae	BE/SI	4	12	3	4	2		1	1				Perennial forb
Trifolium microcephalum	Pursh	Fabaceae	WI/IN	1.4	7	5	1	1.1		1	1			1	Annual forb
Trifolium willdenovii	Spreng.	Fabaceae	WI/IN	1.3	4	3	1	0.6		1	1	1	1	1	Annual forb
Notholithocarpus densiflorus var. *echinoides*	(Hook. & Arn.) Manos, C.H. Cannon, & S. Oh	Fagaceae	SI	2.5	12.3	5	1	2.5		1				1	Shrub
Quercus durata var. *durata*	Jeps.	Fagaceae	SE	5.8	40.5	7	6	0.8			1	1	1	1	Shrub
Quercus vacciniifolia	Kellogg	Fagaceae	SI	2.5	12.3	5	2	2.2		1	1			1	Shrub
Garrya buxifolia	A. Gray	Garryaceae	SE	5.8	29	5	6	0.4		1	1				Shrub
Garrya congdonii	Eastw.	Garryaceae	BE	5	30	6	5.5	1.3		1	1	1		1	Shrub
Gentiana setigera	A. Gray	Gentianaceae	SE	5.8	17.5	3	6	0.3	1B.2	1	1				Perennial forb
Zeltnera trichantha	(Griseb.) G. Mans.	Gentianaceae	SE	5.5	11	2	5.5	-			1	1			Annual forb
Iris bracteata	S. Watson	Iridaceae	SE	5.8	11.5	2	5.5	-	3.3	1					Perennial forb (rhiz.)
Iris innominata	L. F. Hend.	Iridaceae	SE	5.7	17	3	6	0.6	4.3	1					Perennial forb (rhiz.)
Iris macrosiphon	Torr.	Iridaceae	WI/IN	1.1	3.25	3	1	0.9			1	1		1	Perennial forb (rhiz.)
Iris tenuissima ssp. *purdyiformis*	Dykes	Iridaceae	WI	1.5	3	2	1.5	-		1				1	Perennial forb (rhiz.)
Iris thompsonii	R. C. Foster	Iridaceae	BE	4.5	9	2	4.5	-	4.3	1	1				Perennial forb
Acanthomintha duttonii	(Abrams) Jokerst	Lamiaceae	SE	6	30	5	6	0	1B.1			1	1		Annual forb
Acanthomintha ilicifolia	(A. Gray) A. Gray	Lamiaceae	WI/IN	1.3	3	3	0	1.7	1B.1				1		Annual forb
Acanthomintha lanceolata	Curran	Lamiaceae	SI	3.4	16.8	5	3	2.1	4.2			1	1		Annual forb
Acanthomintha obovata ssp. *obovata*	Jeps.	Lamiaceae	BE/SI	3.5	10.5	3	3	2.5	4.2				1		Annual forb
Monardella douglasii	Benth.	Lamiaceae	WI/IN	1	2	2	1	-			1	1	1		Annual forb
Monardella follettii	(Jeps.) Jokerst	Lamiaceae	SE	5.8	34.5	6	6	0.8	1B.2					1	Shrub
Monardella palmeri	A. Gray	Lamiaceae	BE	4.8	28.5	6	6	2.2	1B.2				1		Perennial forb (rhiz.)
Monardella purpurea	Howell	Lamiaceae	SE	6	24	4	6	0			1	1			Perennial forb
Monardella sheltonii	Torr.	Lamiaceae	SI	3	18	6	3	1.7		1	1			1	Perennial forb
Monardella stebbinsii	Hardham & Bartel	Lamiaceae	SE	6	30	5	6	0	1B.2					1	Perennial forb (rhiz.)
Monardella villosa ssp. *villosa*	Benth.	Lamiaceae	SE	6	24	4	6	0					1		Perennial forb (rhiz.)
Monardella viridis	Jeps.	Lamiaceae	WI/IN	1	2	2	1	-	4.3		1				Perennial forb
Salvia sonomensis	Greene	Lamiaceae	WI	1.6	9.5	6	1.5	1.3		1	1	1	1	1	Shrub
Scutellaria antirrhinoides	Benth.	Lamiaceae	WI	2.3	11.5	5	3	1.5		1	1			1	Perennial forb
Stachys pycnantha	Benth.	Lamiaceae	WI	2.2	11	5	1	2.4	CBR	1	1	1	1	1	Perennial forb
Trichostema laxum	A. Gray	Lamiaceae	BE/SI	4	16	4	4.5	2.4		1	1				Annual forb
Trichostema rubisepalum	Elmer	Lamiaceae	SE	5.6	28	5	6	0.9	4.3				1	1	Annual forb
Pinguicula macroceras	Link	Lentibulariaceae	SE	6	18	3	6	0	2B.2	1					Perennial forb (carn.)
Calochortus clavatus var. *clavatus*	S. Watson	Liliaceae	BE	4.5	13.5	3	4	0.6	4.3				1		Perennial forb (bulb)
Calochortus clavatus var. *pallidus*	S. Watson	Liliaceae	WI	1.6	3.1	2		-				1	1		Perennial forb (bulb)
Calochortus elegans	Pursh	Liliaceae	WI	2	4	2	2	-		1					Perennial forb (bulb)
Calochortus fimbriatus	H. P. McDonald	Liliaceae	WI	1.5	4.5	3	1	1.3	1B.3	1	1			1	Perennial forb (bulb)
Calochortus fimbriatus	H. P. McDonald	Liliaceae	WI/IN	1	3	3	0	1.7	1B.3				1		Perennial forb (bulb)
Calochortus nudus	S. Watson	Liliaceae	WI	2.1	8.5	4	2.5	1.2		1				1	Perennial forb (bulb)
Calochortus obispoensis	Lemmon	Liliaceae	BE	5.4	21.5	4	6	1.5	1B.2				1		Perennial forb (bulb)

APPENDIX 1. CONTINUED.

Taxon[1]	Authority	Family	Aff[2]	Mean[3]	Sum[4]	Sourc.	Med[5]	SD[6]	Rarity[7]	Geog. Distribution[8]					Lifeform[9]
										KL	NC	BA	SC	SN	
Calochortus raichei	Farwig & V. Girard	Liliaceae	SE	6	18	3	6	0	1B.2		1				Perennial forb (bulb)
Calochortus tiburonensis	A. J. Hill	Liliaceae	SE	6	24	4	6	0	1B.1		1	1			Perennial forb (bulb)
Calochortus umbellatus	Alph. Wood	Liliaceae	SI	2.9	14.5	5	3	1.1	4.2		1	1			Perennial forb (bulb)
Calochortus uniflorus	Hook. & Arn.	Liliaceae	WI	1.7	5	3	1	1.2	4.2	1	1	1	1		Perennial forb (bulb)
Calochortus vestae	Purdy	Liliaceae	WI	2	6	3	2	1		1	1				Perennial forb (bulb)
Erythronium californicum	Purdy	Liliaceae	SI	2.7	8	3	2	2.1		1	1				Perennial forb (bulb)
Erythronium citrinum var. *citrinum*	S. Watson	Liliaceae	BE/SI	4.3	21.5	5	4	0.4	4.3	1					Perennial forb (bulb)
Erythronium citrinum var. *roderickii*	S. Watson	Liliaceae	BE	4.7	37.5	8	4.5	1.4	1B.3	1					Perennial forb (bulb)
Erythronium helenae	Applegate	Liliaceae	BE	4.5	18	4	4.5	1.7	4.2		1				Perennial forb (bulb)
Erythronium hendersonii	S. Watson	Liliaceae	SI	2.5	5	2	2.5	-	2B.3	1					Perennial forb (bulb)
Erythronium multiscapideum	(Kellogg) A. Nelson & P. B. Kenn.	Liliaceae	SI	3	15	5	2	1.7						1	Perennial forb (bulb)
Erythronium purpurascens	S. Watson	Liliaceae	WI/IN	1	2	2	1	-						1	Perennial forb (bulb)
Erythronium tuolumnense	Applegate	Liliaceae	SI	2.5	5	2	2.5	-	1B.2					1	Perennial forb (bulb)
Fritillaria affinis	(Schult. & Schult. f.) Sealy	Liliaceae	WI	2	6	3	2	0		1	1	1		1	Perennial forb (bulb)
Fritillaria agrestis	Greene	Liliaceae	SI	2.7	13.3	5	2	1.6	4.2		1	1	1	1	Perennial forb (bulb)
Fritillaria biflora var. *biflora*	Lindl.	Liliaceae	WI	2.3	9	4	2.5	1.7	CBR		1	1	1		Perennial forb
Fritillaria biflora var. *ineziana*	Lindl.	Liliaceae	BE	5.4	21.5	4	6	1.5	1B.1			1			Perennial forb (bulb)
Fritillaria eastwoodiae	R. M. MacFarl.	Liliaceae	WI	2.3	13.5	6	2	0.4	3.2					1	Perennial forb (bulb)
Fritillaria falcata	(Jeps.) D. E. Beetle	Liliaceae	SE	6	24	4	6	0	1B.2			1	1		Perennial forb (bulb)
Fritillaria glauca	Greene	Liliaceae	BE/SI	4.3	17.3	4	5.5	2.7	4.2	1	1				Perennial forb
Fritillaria liliacea	Lindl.	Liliaceae	WI	1.8	7	4	1.5	1.1	1B.2			1	1		Perennial forb (bulb)
Fritillaria pluriflora	Torr. ex Benth.	Liliaceae	WI	2.4	9.5	4	2.5	1.5	1B.2		1			1	Perennial forb (bulb)
Fritillaria purdyi	Eastw.	Liliaceae	BE	4.5	31.5	7	4	1.8	4.3	1	1				Perennial forb (bulb)
Fritillaria recurva	Benth.	Liliaceae	SI	2.7	8	3	2.5	1.9		1	1			1	Perennial forb (bulb)
Fritillaria viridea	Kellogg	Liliaceae	SE	6	18	3	6	0	1B.2				1		Perennial forb (bulb)
Lilium bolanderi	S. Watson	Liliaceae	SE	6	18	3	6	0	4.2	1					Perennial forb (bulb)
Lilium kelloggii	Purdy	Liliaceae	SI	2.5	10	4	2	1.9	4.3	1	1				Perennial forb (bulb)
Lilium pardalinum ssp. *vollmeri*	Kellogg	Liliaceae	BE	5	15	3	5	1	4.3	1					Perennial forb (bulb)
Lilium rubescens	S. Watson	Liliaceae	WI	2	9.75	5	2	1.4	4.2	1	1	1			Perennial forb (bulb)
Lilium washingtonianum ssp. *purpurascens*	Kellogg	Liliaceae	BE/SI	3.5	10.5	3	3	2.5	4.3	1					Perennial forb (bulb)
Prosartes parvifolia	S. Watson	Liliaceae	BE	5	5	1	5	-	1B.2	1					Perennial forb
Hesperolinon adenophyllum	(A. Gray) Small	Linaceae	SE	5.7	28.5	5	6	0.9	1B.2		1				Annual forb
Hesperolinon bicarpellatum	(H. Sharsm.) H. Sharsm.	Linaceae	SE	6	18	3	6	0	1B.2		1				Annual forb
Hesperolinon breweri	(A. Gray) Small	Linaceae	SI	2.5	10	4	2.5	1.5	1B.2		1	1			Annual forb
Hesperolinon californicum	(Benth.) Small	Linaceae	SI	2.8	8.5	3	3	0.6			1	1	1	1	Annual forb
Hesperolinon clevelandii	(Greene) Small	Linaceae	WI	2	8	4	2	1.8			1	1			Annual forb
Hesperolinon congestum	(A. Gray) Small	Linaceae	SE	6	24	4	6	0	1B.1		1	1			Annual forb
Hesperolinon didymocarpum	H. Sharsm.	Linaceae	SE	6	18	3	6	0	1B.2		1				Annual forb
Hesperolinon disjunctum	H. Sharsm.	Linaceae	SE	6	18	3	6	0			1	1	1		Annual forb
Hesperolinon drymarioides	(Curran) Small	Linaceae	SE	6	24	4	6	0	1B.2		1				Annual forb
Hesperolinon micranthum	(A. Gray) Small	Linaceae	WI	2.4	11.8	5	3	1		1	1	1	1	1	Annual forb
Hesperolinon sharsmithiae	R. O'Donnell	Linaceae	SE	5.7	17	3	6	0.6			1	1			Annual forb
Hesperolinon spergulinum	(A. Gray) Small	Linaceae	BE	4.7	14	3	6	2.3	CBR		1	1			Annual forb
Hesperolinon tehamense	H. Sharsm.	Linaceae	SE	5.8	34.5	6	6	0.8	1B.3		1				Annual forb
Linum lewisii var. *lewisii*	Pursh	Linaceae	WI/IN	1.3	4	3	1	1.5		1	1	1	1	1	Perennial forb
Fremontodendron decumbens	R. M. Lloyd	Malvaceae	WI	2	8	4	1.5	2.4	1B.2					1	Shrub
Sidalcea asprella ssp. *nana*	Greene	Malvaceae	SI	2.5	5	2.5	2.5	-		1	1			1	Perennial forb
Sidalcea diploscypha	(Torr. & A. Gray) A. Gray	Malvaceae	SI	2.6	13	5	3	2.3			1	1	1	1	Annual forb
Sidalcea hartwegii	A. Gray	Malvaceae	WI	1.6	4.75	3	2	0.7			1			1	Annual forb
Sidalcea hickmanii ssp. *anomala*	Greene	Malvaceae	SE	5.6	22.5	4	6	1	1B.2				1		Perennial forb
Sidalcea hickmanii ssp. *viridis*	Greene	Malvaceae	SE	6	12	2	6	-	1B.1		1	1			Perennial forb
Sidalcea keckii	Wiggins	Malvaceae	SI	3	6	2	3	-	1B.1					1	Annual forb
Pseudotrillium rivale	(S. Watson) S. B Farmer	Melanthiaceae	BE/SI	4	12	3	4	1		1					Perennial forb

APPENDIX 1. CONTINUED.

Taxon[1]	Authority	Family	Aff[2]	Mean[3]	Sum[4]	Sourc.	Med[5]	SD[6]	Rarity[7]	Geog. Distribution[8]					Lifeform[9]
										KL	NC	BA	SC	SN	
Toxicoscordion fontanum	(Eastw.) Zomlefer & Judd	Melanthiaceae	BE/SI	3.8	23	6	4	0.8	4.2		1	1	1		Perennial forb (bulb)
Toxicoscordion paniculatum	(Nutt.) Rydb.	Melanthiaceae	WI	1.6	4.75	3	2	0.7		1	1			1	Perennial forb (bulb)
Xerophyllum tenax	(Pursh) Nutt.	Melanthiaceae	WI	1.6	8	5	1	0.9		1	1	1	1	1	Perennial forb (rhiz.)
Calyptridium quadripetalum	S. Watson	Montiaceae	BE	4.6	27.5	6	4	1.2	4.3		1				Annual forb
Calyptridium umbellatum	(Torr.) Greene	Montiaceae	WI/IN	1.3	4	3	1	1.5		1	1	1		1	Perennial forb
Claytonia exigua ssp. *exigua*	Torr. & A. Gray	Montiaceae	SI	3.4	24	7	3	1.1		1	1	1	1	1	Annual forb
Claytonia exigua ssp. *glauca*	Torr. & A. Gray	Montiaceae	BE/SI	3.6	18	5	3	1.3		1	1	1	1		Annual forb
Claytonia gypsophiloides	Fisch. & C. A. Mey.	Montiaceae	SI	3.1	15.5	5	3	0.2			1	1	1		Annual forb
Claytonia saxosa	Brandegee	Montiaceae	BE/SI	4.4	21.8	5	5	2.2	CBR	1	1				Annual forb
Claytonia serpenticola	T.R. Stoughton	Montiaceae	BE/SI	4	4	1	4	-		1					Perennial forb
Lewisia cantelovii	J. T. Howell	Montiaceae	WI/IN	1	6	6	1	1.1	1B.2	1				1	Perennial forb
Lewisia cotyledon var. *cotyledon*	(S. Watson) B. L. Rob.	Montiaceae	WI	2	6	3	3	1.7	CBR	1					Perennial forb
Lewisia cotyledon var. *heckneri*	(S. Watson) B. L. Rob.	Montiaceae	WI/IN	1	4	4	0.5	1.4	1B.2	1					Perennial forb
Lewisia cotyledon var. *howellii*	(S. Watson) B. L. Rob.	Montiaceae	WI/IN	1.3	4	3	1	1.5	3.2	1					Perennial forb
Lewisia leeana	(Porter) B. L. Rob.	Montiaceae	SI	3	6	2	3	-		1	1			1	Perennial forb
Lewisia nevadensis	(A. Gray) B. L. Rob.	Montiaceae	WI	1.7	5	3	2	1.5		1	1			1	Perennial forb
Lewisia oppositifolia	(S. Watson) B. L. Rob.	Montiaceae	BE	5.3	21	4	6	1.5	2B.2	1					Perennial forb
Lewisia rediviva	Pursh	Montiaceae	WI/IN	1.4	7	5	1	1.1		1	1	1	1	1	Perennial forb
Lewisia stebbinsii	Gankin & W. R. Hildreth	Montiaceae	BE	4.7	14	3	6	2.3			1				Perennial forb
Lewisia triphylla	(S. Watson) B. L. Rob.	Montiaceae	WI	1.7	5	3	2	1.5		1	1			1	Perennial forb
Camissonia benitensis	P. H. Raven	Onagraceae	SE	5.9	29.5	5	6	0.4	1B.1				1		Annual forb
Camissonia lacustris	P. H. Raven	Onagraceae	SI	3	9	3	3	3			1			1	Annual forb
Clarkia arcuata	(Kellogg) A. Nelson & J. F. Macbr.	Onagraceae	WI	2.3	7	3	2	0.6						1	Annual forb
Clarkia biloba ssp. *biloba*	(Durand) A. Nelson & J. F. Macbr.	Onagraceae	WI/IN	1.4	2.75	2	1.4	-				1		1	Annual forb
Clarkia breweri	(A. Gray) Greene	Onagraceae	BE/SI	3.8	11.5	3	3	2.1	4.2			1	1		Annual forb
Clarkia franciscana	H. Lewis & P. H. Raven	Onagraceae	SE	6	24	4	6	0	1B.1			1	1		Annual forb
Clarkia gracilis ssp. *albicaulis*	(Piper) A. Nelson & J. F. Macbr.	Onagraceae	WI	2.2	6.5	3	2	1	1B.2					1	Annual forb
Clarkia gracilis ssp. *tracyi*	(Piper) A. Nelson & J. F. Macbr.	Onagraceae	BE	5	25	5	5	1	4.2		1				Annual forb
Epilobium minutum	Lindl.	Onagraceae	WI	2	6	3	2	1		1	1	1	1	1	Annual forb
Epilobium oreganum	Greene	Onagraceae	BE/SI	3.8	23	6	4	2.2	1B.2	1	1				Perennial forb
Epilobium rigidum	Hausskn.	Onagraceae	BE	5.1	20.5	4	6	2	4.3	1					Perennial forb
Epilobium septentrionale	(D. D. Keck) R. N. Bowman & Hoch	Onagraceae	WI	2	4	2		-	4.3		1				Perennial forb
Epilobium siskiyouense	(Munz) Hoch & P. H. Raven	Onagraceae	SE	5.5	38.5	7	6	1	1B.3	1					Perennial forb
Cypripedium californicum	A. Gray	Orchidaceae	BE	4.5	40.5	9	4	1.3	4.2	1	1	1		1	Perennial forb (bulb)
Cypripedium fasciculatum	Kellogg	Orchidaceae	SI	2.5	12.3	5	2	1.6	4.2	1	1	1		1	Perennial forb (bulb)
Piperia candida	Rand. Morgan & Ackerman	Orchidaceae	WI/IN	1.2	3.5	3	1	1	1B.2	1	1	1			Perennial forb (bulb)
Aphyllon validum ssp. *howellii*	Jeps.	Orobanchaceae	SI	3.4	13.5	4	3	1.3	4.3		1				Perennial forb (paras.)
Castilleja affinis ssp. *neglecta*	Hook. & Arn.	Orobanchaceae	SE	6	30	5	6	0			1	1			Perennial forb (hemipar.)
Castilleja brevilobata	Piper	Orobanchaceae	SE	6	18	3	6	0	4.2	1					Perennial forb (hemipar.)
Castilleja foliolosa	Hook. & Arn.	Orobanchaceae	WI	2.3	9	4	2.5	1			1	1	1	1	Perennial forb, Shrub
Castilleja miniata ssp. *elata*	Douglas ex Hook.	Orobanchaceae	BE	4.6	27.5	6	4.5	1.4		1					Perennial forb (hemipar.)
Castilleja minor ssp. *spiralis*	(A. Gray) A. Gray	Orobanchaceae	SI	3.3	16.5	5	3	2.6			1	1	1	1	Annual forb (hemipar.)
Castilleja pruinosa	Fernald	Orobanchaceae	SI	3.2	15.8	5	3	1.9		1	1			1	Perennial forb (hemipar.)
Castilleja rubicundula ssp. *lithospermoides*	(Jeps.) T. I. Chuang & Heckard	Orobanchaceae	WI	2.4	9.75	4	2	1.8			1				Annual forb (hemipar.)
Castilleja rubicundula ssp. *rubicundula*	(Jeps.) T. I. Chuang & Heckard	Orobanchaceae	SE	5.6	28	5	6	0.9			1				Annual forb (hemipar.)
Cordylanthus nidularius	J. T. Howell	Orobanchaceae	SE	6	18	3	6	0	1B.1			1	1		Annual forb (hemipar.)
Cordylanthus pilosus ssp. *pilosus*	A. Gray	Orobanchaceae	SI	2.5	10	4	2.5	0.6			1	1			Annual forb (hemipar.)

APPENDIX 1. CONTINUED.

Taxon[1]	Authority	Family	Aff[2]	Mean[3]	Sum[4]	Sourc.	Med[5]	SD[6]	Rarity[7]	Geog. Distribution[8]					Lifeform[9]
										KL	NC	BA	SC	SN	
Cordylanthus pringlei	A. Gray	Orobanchaceae	SE	5.6	28	5	6	0.9	CBR		1				Annual forb (hemipar.)
Cordylanthus tenuis ssp. *brunneus*	A. Gray	Orobanchaceae	BE	5.1	25.5	5	5	1	4.3		1				Annual forb (hemipar.)
Cordylanthus tenuis ssp. *capillaris*	A. Gray	Orobanchaceae	SE	6	24	4	6	0	1B.2		1				Annual forb (hemipar.)
Cordylanthus tenuis ssp. *tenuis*	A. Gray	Orobanchaceae	WI	2.3	9	4	2	0.5						1	Annual forb (hemipar.)
Cordylanthus tenuis ssp. *viscidus*	A. Gray	Orobanchaceae	BE	4.5	27	6	4.5	1.4		1	1			1	Annual forb (hemipar.)
Orthocarpus pachystachyus	A. Gray	Orobanchaceae	SE	6	18	3	6	0	1B.1	1					Annual forb (hemipar.)
Pedicularis howellii	A. Gray	Orobanchaceae	SI	2.5	7.5	3	3	1.2	4.3	1					Perennial forb (hemipar.)
Triphysaria floribunda	(Benth.) T. I. Chuang & Heckard	Orobanchaceae	WI	2.3	6.75	3	2	1.9	1B.2		1	1	1		Annual forb
Dicentra formosa ssp. *oregana*	(Haw.) Walp.	Papaveraceae	BE	5.2	31	6	6	1.3	4.2	1					Perennial forb
Dicentra pauciflora	S. Watson	Papaveraceae	WI	2.2	6.5	3	3	1.4	CBR	1				1	Perennial forb
Ehrendorferia chrysantha	(Hook. & Arn.) Rylander	Papaveraceae	WI/IN	1.1	3.25	3	1	0.9		1	1	1	1	1	Perennial forb
Eschscholzia hypecoides	Benth.	Papaveraceae	SI	2.6	7.75	3	1	3.1	4.3				1		Annual forb
Platystemon californicus	Benth.	Papaveraceae	WI	1.7	5	3	2	0.6		1	1	1	1	1	Annual forb
Parnassia cirrata var. *intermedia*	Piper	Parnassiaceae	BE/SI	3.5	7	2	3.5	-		1					Perennial forb
Parnassia palustris	L.	Parnassiaceae	WI	2	6	3	2	0		1	1		1	1	Perennial forb
Diplacus douglasii	(Benth.) G.L. Nesom	Phrymaceae	SI	2.7	13.5	5	3	0.5		1	1	1	1	1	Annual forb
Diplacus layneae	(Greene) Jeps.	Phrymaceae	SI	2.9	14.3	5	3	1.2		1	1			1	Annual forb
Erythranthe glaucescens	(Greene) G.L. Nesom	Phrymaceae	BE/SI	3.8	18.8	5	4	2.1						1	Annual forb
Erythranthe linearifolia	Benth.	Phrymaceae	BE/SI	4	16	4	4.5	2.4		1					Perennial forb (rhiz.)
Erythranthe nudata	(Curran ex Greene) G.L. Nesom	Phrymaceae	SE	5.6	33.5	6	6	1.2			1				Annual forb
Erythranthe percaulis	G.L. Nesom	Phrymaceae	SE	6	18	3	6	0	1B.1					1	Annual forb
Erythranthe trinitiensis	G.L. Nesom	Phrymaceae	SE	6	18	3	6	0	1B.3	1	1				Annual forb
Erythranthe willisii	G.L. Nesom	Phrymaceae	SE	5.5	11	2	5.5	-						1	Perennial forb
Picea breweriana	S. Watson	Pinaceae	WI	2.2	6.5	3	3	1.4	CBR	1					Tree
Pinus attenuata	Lemmon	Pinaceae	SI	2.5	12.6	5	3	2.4		1	1	1	1	1	Tree
Pinus balfouriana ssp. *balfouriana*	Grev. & Balf.	Pinaceae	BE/SI	4.3	26	6	4	1.5		1					Tree
Pinus coulteri	D. Don	Pinaceae	WI/IN	1.3	4	3	1	1.5				1	1		Tree
Pinus jeffreyi	Grev. & Balf.	Pinaceae	SI	2.7	8	3	3	0.6		1	1		1	1	Tree
Pinus sabiniana	D. Don	Pinaceae	WI/IN	1.4	4.25	3	1	1.4		1	1	1	1	1	Tree
Antirrhinum cornutum	Benth.	Plantaginaceae	WI	2.2	11	5	2	0.8	CBR		1				Annual forb
Antirrhinum leptaleum	A. Gray	Plantaginaceae	WI	1.6	3.1	2	1.6	-						1	Annual forb
Antirrhinum subcordatum	A. Gray	Plantaginaceae	BE/SI	4.3	21.5	5	4	1.8	4.3		1				Annual forb
Antirrhinum vexillocalyculatum	Kellogg	Plantaginaceae	SI	2.5	20	8	2.5	1.3		1	1	1	1	1	Annual forb
Antirrhinum virga	A. Gray	Plantaginaceae	SI	2.8	8.5	3	3	0.6	4.3		1				Perennial forb
Collinsia greenei	A. Gray	Plantaginaceae	BE	5.2	31	6	6	1.3	CBR	1	1				Annual forb
Collinsia multicolor	Lindl. & Paxton	Plantaginaceae	WI/IN	1.1	2.25	2	1.1	-	1B.2		1	1			Annual forb
Collinsia sparsiflora	Fisch. & C. A. Mey.	Plantaginaceae	WI	1.7	5	3	1	1.2		1	1	1	1	1	Annual forb
Keckiella lemmonii	(A. Gray) Straw	Plantaginaceae	WI/IN	1.1	3.25	3	1	0.9		1	1			1	Shrub
Penstemon azureus var. *azureus*	Benth.	Plantaginaceae	SI	2.7	8	3	3	0.6		1	1			1	Perennial forb
Penstemon filiformis	(D. D. Keck) D. D. Keck	Plantaginaceae	BE	5	30	6	5.5	1.3	1B.3	1					Perennial forb
Penstemon parvulus	(A. Gray) Krautter	Plantaginaceae	BE/SI	3.7	11	3	4	0.6		1				1	Perennial forb
Penstemon purpusii	Brandegee	Plantaginaceae	SI	2.8	11	4	2	2.4	CBR	1	1				Perennial forb
Plantago erecta	E. Morris	Plantaginaceae	WI/IN	1	3	3	1	1		1	1	1	1	1	Annual forb
Veronica copelandii	Eastw.	Plantaginaceae	SE	6	34	4	6	0	4.3	1					Perennial forb
Agrostis microphylla	Steud.	Poaceae	WI/IN	1.1	4.25	4	1.1	1.1			1	1	1		Annual gram.
Bromus laevipes	Shear	Poaceae	WI	1.7	5	3	2	0.6		1	1	1	1	1	Perennial gram. (cesp.)
Calamagrostis foliosa	Kearney	Poaceae	WI	1.7	5	3	2	1.5	4.2		1				Perennial gram. (rhiz.)
Calamagrostis ophitidis	(J. T. Howell) Nygren	Poaceae	SE	6	24	4	6	0	4.3		1	1			Perennial gram. (rhiz.)
Calamagrostis stricta ssp. *inexpansa*	(Timm) Koeler	Poaceae	WI	1.5	3	2	1.5	-		1	1	1	1	1	Perennial gram. (cesp.)
Danthonia californica	Bol.	Poaceae	SI	3.3	13	4	3	2.2		1	1	1	1	1	Perennial gram. (cesp.)
Elymus trachycaulus ssp. *trachycaulus*	(Link) Shinners	Poaceae	WI	1.6	3.1	2	1.6	-		1	1	1	1	1	Perennial gram. (cesp.)
Festuca californica	Vasey	Poaceae	WI	2.4	11.8	5	2	1.6		1	1	1	1	1	Perennial gram. (cesp.)

APPENDIX 1. CONTINUED.

Taxon[1]	Authority	Family	Aff[2]	Mean[3]	Sum[4]	Sourc.	Med[5]	SD[6]	Rarity[7]	Geog. Distribution[8]					Lifeform[9]
										KL	NC	BA	SC	SN	
Festuca idahoensis	Elmer	Poaceae	WI/IN	1.3	5.25	4	1	1.2		1	1	1	1	1	Perennial gram. (cesp.)
Hordeum brachyantherum ssp. *californicum*	Nevski	Poaceae	SI	3.1	9.25	3	3	2.9		1	1	1	1	1	Perennial gram. (cesp.)
Melica geyeri	Munro	Poaceae	WI/IN	1.2	6	5	1	0.4		1	1		1	1	Perennial gram. (cesp.)
Poa piperi	Hitchc.	Poaceae	BE	5.4	21.5	4	5.5	1	4.3	1					Perennial gram. (rhiz.)
Poa rhizomata	Hitchc.	Poaceae	WI	1.8	3.5	2	1.5	-	4.3	1					Perennial gram. (rhiz.)
Poa tenerrima	Scribn.	Poaceae	SI	3.3	13	4	3	1.3	CBR			1	1	1	Perennial gram. (cesp.)
Scribneria bolanderi	(Thurb.) Hack.	Poaceae	WI	1.7	5.1	3	1	2		1	1	1	1	1	Annual gram.
Stipa lemmonii var. *pubescens*	(Vasey) Scribn.	Poaceae	BE	4.8	14.5	3	6	2.3	3.2	1	1				Perennial gram. (cesp.)
Stipa nelsonii var. *dorei*	Scribn.	Poaceae	WI/IN	1	2	2	1	-						1	Perennial gram. (cesp.)
Stipa stillmanii	Bol.	Poaceae	WI/IN	1.1	2.1	2	1.1	-	CBR					1	Perennial gram. (cesp.)
Collomia diversifolia	Greene	Polemoniaceae	SE	5.6	33.5	6	6	1.2	4.3		1	1			Annual forb
Collomia tinctoria	Kellogg	Polemoniaceae	WI	1.8	7.1	4	2	1.5		1	1			1	Annual forb
Gilia capitata ssp. *capitata*	Sims	Polemoniaceae	WI	1.6	4.75	3	1	1.2		1	1				Annual, Perennial forb
Leptosiphon ambiguus	(Rattan) J. M. Porter & L. A. Johnson	Polemoniaceae	SE	5.8	17.5	3	6	0.6				1	1		Annual forb
Leptosiphon bolanderi	(A. Gray) J.M. Porter & L.A. Johnson	Polemoniaceae	WI/IN	1.3	2.5	2	1.3	-			1	1		1	Annual forb
Leptosiphon latisectus	(E. G. Buxton) J. M. Porter & L. A. Johnson	Polemoniaceae	WI	2	6	3	2	0			1				Annual forb
Leptosiphon liniflorus	(Benth.) J. M. Porter & L. A. Johnson	Polemoniaceae	WI	1.6	6.25	4	1.5	1.2		1	1	1	1	1	Annual forb
Leptosiphon nuttallii ssp. *howellii*	(A. Gray) J. M. Porter & L. A. Johnson	Polemoniaceae	BE	5.3	31.5	6	6	1.3			1				Perennial forb
Linanthus dichotomus	Benth.	Polemoniaceae	SI	2.5	12.4	5	3	2.4		1	1	1	1	1	Annual forb
Navarretia heterodoxa	(Greene) Greene	Polemoniaceae	SI	2.8	14	5	3	2.4				1			Annual forb
Navarretia jepsonii	V. L. Bailey ex Jeps.	Polemoniaceae	SE	5.6	22.5	4	5.5	0.6	4.3		1				Annual forb
Navarretia linearifolia ssp. *pinnatisecta*	(Howell) L.A. Johnson	Polemoniaceae	BE/SI	3.8	19	5	3	2.2			1				Annual, Perennial forb
Navarretia mitracarpa	Greene	Polemoniaceae	SE	5.9	23.5	4	6	0.5					1		Annual forb
Navarretia paradoxiclara	L.A. Johnson & D. Gowen	Polemoniaceae	SE	6	18	3	6	0	1B.3					1	Annual forb
Navarretia paradoxinota	L.A. Johnson & D. Gowen	Polemoniaceae	SE	6	18	3	6	0	1B.3		1				Annual forb
Navarretia pubescens	(Benth.) Hook. & Arn.	Polemoniaceae	WI	2	6	3	2	1			1	1	1	1	Annual forb
Navarretia rosulata	Brand	Polemoniaceae	SE	6	18	3	6	0	1B.2		1	1			Annual forb
Navarretia sinistra	(M. E. Jones) L. A. Johnson	Polemoniaceae	SI	2.5	7.5	3	3	1.8		1	1			1	Annual forb
Phlox hirsuta	E. E. Nelson	Polemoniaceae	SE	6	18	3	6	0	1B.2	1					Perennial forb
Polemonium chartaceum	H. Mason	Polemoniaceae	WI	1.6	8.1	5	2	1.5	1B.3	1				1	Perennial forb
Polemonium eddyense	Stubbs	Polemoniaceae	SE	6	18	3	6	0	1B.2	1					Perennial forb
Polygala cornuta var. *cornuta*	Kellogg	Polygalaceae	WI	2.3	9	4	2	1.3		1				1	Perennial forb, shrub
Chorizanthe breweri	S. Watson	Polygonaceae	BE	5.4	21.5	4	5.5	1	1B.3				1		Annual forb
Chorizanthe palmeri	S. Watson	Polygonaceae	BE	4.9	24.5	5	6	1.6	4.2				1		Annual forb
Chorizanthe uniaristata	Torr. & A. Gray	Polygonaceae	SI	2.7	10.8	4	2.5	2					1	1	Annual, Perennial forb
Chorizanthe ventricosa	Goodman	Polygonaceae	BE	5.3	16	3	6	1.2	4.3				1		Annual forb
Eriogonum alpinum	Engelm.	Polygonaceae	SE	6	30	5	6	0	1B.2	1					Perennial forb
Eriogonum argillosum	J. T. Howell	Polygonaceae	SI	3.1	12.5	4	3	2.6	4.3			1	1		Annual forb
Eriogonum cedrorum	Reveal & Raiche	Polygonaceae	SE	6	12	2	6	-	1B.3		1				Perennial forb
Eriogonum clavatum	Small	Polygonaceae	SI	3.3	10	3	3	2.5					1		Annual forb
Eriogonum compositum var. *compositum*	Douglas ex Benth.	Polygonaceae	WI	1.7	5.1	3	2	1.5	CBR	1	1				Perennial forb
Eriogonum congdonii	(S. Stokes) Reveal	Polygonaceae	BE	5.1	35.5	7	6	1.7	4.3	1					Shrub
Eriogonum covilleanum	Eastw.	Polygonaceae	SI	3	12	4	3	1.6	CBR				1		Annual forb
Eriogonum dasyanthemum	Torr. & A. Gray	Polygonaceae	SI	3	6	2	3	-	CBR		1				Annual forb
Eriogonum diclinum	Rev.	Polygonaceae	SI	3.2	9.5	3	3	3	2B.3	1					Perennial forb
Eriogonum elatum var. *villosum*	Douglas ex Benth.	Polygonaceae	SI	3.3	13	4	3.5	3.2		1				1	Perennial forb
Eriogonum hirtellum	J. T. Howell & Bacig.	Polygonaceae	SE	6	18	3	6	0	1B.3	1					Perennial forb (rhiz.)
Eriogonum hirtiflorum	A. Gray ex S. Watson	Polygonaceae	SI	3.3	13	4	3.5	3.2	CBR	1	1	1	1	1	Annual forb

APPENDIX 1. CONTINUED.

Taxon[1]	Authority	Family	Aff[2]	Mean[3]	Sum[4]	Sourc.	Med[5]	SD[6]	Rarity[7]	Geog. Distribution[8]					Lifeform[9]
										KL	NC	BA	SC	SN	
Eriogonum kelloggii	A. Gray	Polygonaceae	SE	6	24	4	6	0	1B.2		1				Perennial forb
Eriogonum libertini	Reveal	Polygonaceae	SE	6	36	6	6	0	4.2	1	1				Perennial forb
Eriogonum luteolum var. *caninum*	Greene	Polygonaceae	SE	5.5	27.5	5	6	0.9	1B.2		1	1			Annual forb
Eriogonum luteolum var. *luteolum*	Greene	Polygonaceae	BE/SI	3.8	15	4	3	1.5		1	1	1		1	Annual forb
Eriogonum luteolum var. *pedunculatum*	Greene	Polygonaceae	BE	5	10	2	5	-	CBR					1	Annual forb
Eriogonum nervulosum	(S. Stokes) Reveal	Polygonaceae	SE	6	18	3	6	0	1B.2		1				Perennial forb (rhiz.)
Eriogonum nudum var. *indictum*	Douglas ex Benth.	Polygonaceae	WI	1.5	4.5	3	1	0.6	4.2				1		Perennial forb
Eriogonum nudum var. *oblongifolium*	Douglas ex Benth.	Polygonaceae	WI	2	6	3	2	0		1	1			1	Perennial forb
Eriogonum pendulum	S. Watson	Polygonaceae	SE	6	18	3	6	0	2B.2	1					Perennial forb
Eriogonum pyrolifolium	Hook.	Polygonaceae	WI/IN	1	3	3	0	1.7		1				1	Perennial forb
Eriogonum siskiyouense	Small	Polygonaceae	BE	5.4	32.5	6	6	1.2	4.3	1					Perennial forb
Eriogonum strictum var. *greenei*	Benth.	Polygonaceae	SE	5.9	29.5	5	6	0.4	4.3	1	1				Perennial forb
Eriogonum ternatum	Howell	Polygonaceae	SE	6	18	3	6	0	4.3	1	1				Perennial forb
Eriogonum tripodum	Greene	Polygonaceae	BE	5.3	26.5	5	6	1.3	4.2		1			1	Shrub
Eriogonum umbellatum var. *argus*	Torr.	Polygonaceae	SI	3	12	4	3.5	1.4	CBR	1	1				Perennial forb
Eriogonum umbellatum var. *bahiiforme*	Torr.	Polygonaceae	BE/SI	3.5	21	6	3	1.2	4.2		1	1	1		Perennial forb
Eriogonum umbellatum var. *goodmanii*	Torr.	Polygonaceae	SI	3.3	10	3	3	2.5	CBR	1					Perennial forb
Eriogonum umbellatum var. *humistratum*	Torr.	Polygonaceae	BE	4.5	27.3	6	5	2.1	4.3	1	1				Perennial forb
Eriogonum umbellatum var. *nelsoniorum*	Torr.	Polygonaceae	SE	5.5	11	2	5.5	-		1	1				Perennial forb
Eriogonum umbellatum var. *speciosum*	Torr.	Polygonaceae	BE/SI	4.2	21	5	4	1.3	CBR	1				1	Perennial forb
Eriogonum ursinum	S. Watson	Polygonaceae	WI/IN	1.1	2.25	2	1.1	-		1				1	Perennial forb
Eriogonum vimineum	Douglas ex Benth.	Polygonaceae	WI/IN	1	3	3	1	0		1				1	Annual forb
Polygonum majus	(Meisn.) Piper	Polygonaceae	WI	1.5	4.5	3	2	0.9		1				1	Annual forb
Polygonum spergulariiforme	Meisn. ex Small	Polygonaceae	SI	3	18.3	6	2.5	2.1		1	1	1		1	Annual forb
Systenotheca vortriedei	(Brandegee) Reveal & Hardham	Polygonaceae	SI	3.1	12.3	4	2.5	2.2	4.3				1		Annual forb
Primula clevelandii var. *patula*	(Greene) Mast & Reveal	Primulaceae	SI	3	9	3	3	0				1	1	1	Perennial forb
Adiantum aleuticum	(Rupr.) C. A. Paris	Pteridaceae	WI	2.4	11.8	5	2	1.2		1	1	1	1	1	Perennial forb
Aspidotis carlotta-halliae	(W. H. Wagner & E. F. Gilbert) Lellinger	Pteridaceae	BE	5.3	26.5	5	6	1.1	4.2			1	1		Perennial forb (rhiz.)
Aspidotis densa	(Brack.) Lellinger	Pteridaceae	SI	3.4	31	9	3	1.2		1	1	1	1	1	Perennial forb
Pellaea brachyptera	(T. Moore) Baker	Pteridaceae	WI	1.5	4.5	3	2	0.9		1	1			1	Perennial forb
Anemone drummondii var. *drummondii*	S. Watson	Ranunculaceae	WI	2.3	6.75	3	2	1.6		1				1	Perennial forb
Anemone oregana var. *oregana*	A. Gray	Ranunculaceae	SI	3	6	2	3	-		1					Perennial forb
Aquilegia eximia	Van Houtte ex Planch..	Ranunculaceae	BE/SI	4.2	25	6	3.5	1.5			1	1	1		Perennial forb
Delphinium hesperium ssp. *hesperium*	A. Gray	Ranunculaceae	SI	2.7	8	3	3	0.6		1	1	1			Perennial forb
Delphinium nuttallianum	Pritz.	Ranunculaceae	WI/IN	1.4	4.1	3	1	1.5		1				1	Perennial forb
Delphinium parryi ssp. *eastwoodiae*	A. Gray	Ranunculaceae	BE/SI	3.7	11	3	4	2.5	1B.2				1		Perennial forb
Delphinium uliginosum	Curran	Ranunculaceae	SE	5.7	28.5	5	6	0.9	4.2		1				Perennial forb
Ceanothus arcuatus	McMinn	Rhamnaceae	BE/SI	3.5	7	2	3.5	-		1	1			1	Shrub
Ceanothus confusus	J. T. Howell	Rhamnaceae	WI/IN	1.3	2.5	2	1.3	-	1B.1		1				Shrub
Ceanothus cuneatus var. *cuneatus*	(Hook.) Nutt.	Rhamnaceae	WI	1.5	6.1	4	1.5	1.3		1	1	1	1	1	Shrub
Ceanothus divergens	Parry	Rhamnaceae	WI	2	4	2	2	-	1B.2		1				Shrub
Ceanothus ferrisiae	McMinn	Rhamnaceae	SE	6	24	4	6	0	1B.1			1			Shrub
Ceanothus foliosus var. *medius*	Parry	Rhamnaceae	BE/SI	4	12	3	3	1.7				1	1		Shrub
Ceanothus jepsonii	Greene	Rhamnaceae	SE	6	18	3	6	0			1	1			Shrub
Ceanothus masonii	McMinn	Rhamnaceae	SI	3.3	6.5	2	3	-	1B.2			1			Shrub
Ceanothus pumilus	Greene	Rhamnaceae	SE	5.7	28.5	5	6	0.9		1	1				Shrub
Ceanothus roderickii	W. Knight	Rhamnaceae	WI	1.7	5	3	2	1.5	1B.1					1	Shrub
Ceanothus sonomensis	J. T. Howell	Rhamnaceae	WI/IN	1.3	4	3	2	1.2	1B.2			1			Shrub
Frangula californica ssp. *crassifolia*	(Eschsch.) A. Gray	Rhamnaceae	BE	4.8	19	4	6	2.5		1	1				Shrub
Frangula californica ssp. *occidentalis*	(Eschsch.) A. Gray	Rhamnaceae	SE	6	24	4	6	0		1	1			1	Shrub
Frangula californica ssp. *tomentella*	(Eschsch.) A. Gray	Rhamnaceae	WI	1.5	6	4	0.8	1.7		1	1	1	1	1	Shrub
Adenostoma fasciculatum	Hook. & Arn.	Rosaceae	WI/IN	1.3	5.2	4	1.1	1.4			1	1	1	1	Shrub

APPENDIX 1. CONTINUED.

										Geog. Distribution[8]					
Taxon[1]	Authority	Family	Aff[2]	Mean[3]	Sum[4]	Sourc.	Med[5]	SD[6]	Rarity[7]	KL	NC	BA	SC	SN	Lifeform[9]
Holodiscus discolor	(Pursh) Maxim.	Rosaceae	WI/IN	1	3	3	1	1		1	1	1	1	1	Shrub
Horkelia congesta var. *nemorosa*	Hook.	Rosaceae	BE/SI	3.8	7.5	2	3.5	-	2B.1	1					Perennial forb
Horkelia daucifolia	(Greene) Rydb.	Rosaceae	BE/SI	3.8	15	4	3	1.5		1	1				Perennial forb
Horkelia daucifolia var. *daucifolia*	(Greene) Rydb.	Rosaceae	BE	4.5	9	2	4.5	-		1					Perennial forb
Horkelia sericata	S. Watson	Rosaceae	SE	5.6	22.5	4	6	1	4.3	1					Perennial forb
Horkelia tridentata var. *flavescens*	Torr.	Rosaceae	SI	3	9	3	2	1.7		1	1			1	Perennial forb
Ivesia gordonii	(Hook.) Torr. & A. Gray	Rosaceae	WI	1.6	3.25	2	1.6	-		1	1			1	Perennial forb
Ivesia pickeringii	Torr. ex A. Gray	Rosaceae	BE	5.4	32.5	6	6	1	1B.2	1					Perennial forb
Potentilla cristae	Ferlatte & Strother	Rosaceae	SI	3.1	12.5	4	3	0	1B.3	1					Perennial forb
Sanguisorba officinalis	L.	Rosaceae	BE/SI	4.2	12.5	3	3	1.7	2B.2	1	1				Perennial forb (rhiz.)
Galium ambiguum ssp. *ambiguum*	W. Wight	Rubiaceae	SI	3.3	10	3	3	2.5			1			1	Perennial forb
Galium ambiguum ssp. *siskiyouense*	W. Wight	Rubiaceae	SE	5.5	27.5	5	6	0.9		1	1				Perennial forb
Galium andrewsii ssp. *andrewsii*	A. Gray	Rubiaceae	SI	3.2	16	5	3	1.9			1	1	1		Perennial forb
Galium andrewsii ssp. *gatense*	A. Gray	Rubiaceae	BE	5.1	20.5	4	5	0.8	4.2			1	1		Perennial forb
Galium andrewsii ssp. *intermedium*	A. Gray	Rubiaceae	WI/IN	1.4	2.75	2	1.4	-					1		Perennial forb
Galium clementis	Eastw.	Rubiaceae	WI/IN	1	2	2	1	-	1B.3				1		Perennial forb
Galium hardhamiae	Dempster	Rubiaceae	SE	6	24	4	6	0	1B.3				1		Perennial forb
Galium serpenticum ssp. *scotticum*	Dempster	Rubiaceae	SE	5.9	29.5	5	6	0.4	1B.2	1					Perennial forb
Salix breweri	Bebb	Salicaceae	SE	6	30	5	6	0			1	1	1		Shrub
Salix delnortensis	C. K. Schneid.	Salicaceae	SE	6	18	3	6	0	4.3	1					Shrub
Salix sitchensis	Sanson ex Bong.	Salicaceae	WI	1.6	4.75	3	1	1.2		1	1	1	1		Tree, shrub
Darlingtonia californica	Torr.	Sarraceniaceae	BE/SI	4.1	32.5	8	4	1.4	4.2	1				1	Perennial forb (carn.)
Micranthes howellii	(Greene) Small	Saxifragaceae	BE/SI	3.8	7.5	2	3.5	-	4.3	1					Perennial forb
Odontostomum hartwegii	Torr.	Tecophilaeaceae	SI	2.7	8	3	3	0.6			1			1	Perennial forb
Brodiaea rosea ssp. *rosea*	(Greene) Baker	Themidaceae	BE/SI	4	12	3	4	2	3.1	1	1				Perennial forb
Brodiaea sierrae	R. E. Preston	Themidaceae	WI	1.7	5	3	1	1.7	4.3					1	Perennial forb
Brodiaea stellaris	S. Watson	Themidaceae	BE/SI	3.7	11	3	4	2.5			1				Perennial forb
Muilla maritima	(Torr.) S. Watson	Themidaceae	WI	2	6	3	2	1			1	1	1	1	Perennial forb
Triteleia bridgesii	(S. Watson) Greene	Themidaceae	SI	3.3	13	4	3.5	1.7		1	1			1	Perennial forb
Triteleia crocea	(Alph. Wood) Greene	Themidaceae	BE/SI	4.1	32.5	8	3.7	1.8		1					Perennial forb
Triteleia ixioides ssp. *cookii*	(W. T. Aiton) Greene	Themidaceae	BE	4.5	13.5	3	6	2.9	1B.3				1		Perennial forb
Triteleia peduncularis	Lindl.	Themidaceae	BE/SI	3.8	19	5	3	2.2		1	1	1	1		Perennial forb
Verbena californica	Moldenke	Verbenaceae	BE	4.8	14.5	3	4	1.2	1B.1					1	Perennial forb
Viola cuneata	S. Watson	Violaceae	BE	5.2	31	6	6	1.3	CBR	1	1				Perennial forb
Viola douglasii	Steud.	Violaceae	SI	2.8	13.8	5	2	2		1	1	1	1	1	Perennial forb
Viola hallii	A. Gray	Violaceae	BE/SI	4	16	4	4	2.3	CBR	1	1				Perennial forb
Viola lobata ssp. *lobata*	Benth.	Violaceae	WI	2.3	11.4	5	2	2.4		1	1			1	Perennial forb (rhiz.)
Viola ocellata	Torr. & A. Gray	Violaceae	SI	2.5	12.5	5	3	0.9		1	1	1	1		Perennial forb
Viola primulifolia ssp. *occidentalis*	L.	Violaceae	BE	5.1	25.5	5	6	1.4	1B.2	1					Perennial forb (rhiz.)
Viola purpurea ssp. *integrifolia*	Kellogg	Violaceae	WI/IN	1.3	4	3	2	1.2		1	1			1	Perennial forb

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GERMINATION OF MULTI-YEAR COLLECTIONS OF CALIFORNIA GRASSLAND AND SCRUB SEEDS

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Abstract

Successful restoration of California terrestrial ecosystems requires knowledge of seed germination rates for a diversity of native species. We quantified greenhouse germination of 25 native perennial forbs, shrubs, and grasses collected coastally near Santa Cruz, CA for restoration at the Younger Lagoon Reserve and nine annual forb species from interior grasslands at Pinnacles National Park. Seeds of most species were collected in multiple years. Twenty-seven of our 34 study species had at least 25% germination without complicated germination triggers. All but two of the 13 species that were collected in ≥3 years and germinated showed significant interannual variation in germination; seven species had a trend of decreasing percent germination with increasing age. These species- and collection-year specific results indicate a necessity to test seed stock when possible prior to seeding to increase restoration success, and highlight the importance of following best practices for seed collection and storage.

Key Words: central California, coastal prairie, grassland, restoration, sage scrub, seed germination, seed longevity.

Sage scrub and grassland ecosystems are critically threatened in California (Hoekstra et al. 2005) due to land conversion, non-native invasive species, and altered disturbance regimes (Vasey and Holl 2007). The long-term recovery of California native ecosystems depends on developing best management strategies for their restoration, in particular propagating and planting native seed to ensure conservation of biodiversity and genetic diversity at the project site and increasing site resistance to invasive species (Stromberg et al. 2007; Vasey and Holl 2007). Restoration requires species-specific information on seed germination rates and seed longevity data for the huge variety of California native species.

Seed germination rates are determined by many variables including seed age, storage practices, maternal effects, climate, and site conditions (Rajjou et al. 2008; Baskin and Baskin 2014). Past studies of orthodox seeds, i.e., seeds that survive drying and/or freezing events in storage, have shown that many species retain viability for decades, whereas seed viability decreases rapidly over time for other species (Priestley et al. 1985; Walters et al. 2005; Fenner 2017). Furthermore, a number of past studies have found reduced seed longevity over time when seeds are exposed to conditions with higher moisture and temperature (Dickie et al. 1988; Brown and Briggs 1991; Nguyen et al. 2012). Maternally expressed genetic factors strongly influence seed development and resulting seed mass, which both influence resulting germination (Wulff 1995; Wang et al. 2016). Likewise, site conditions (e.g., soil moisture and nutrients) can affect seed germination (Fenner 2017).

This study aimed to quantify the percent germination of 34 native California grassland and coastal species that are commonly used in restoration projects in central California, most of which were collected in multiple years. Our results supplement existing information on seed germination requirements and rates (e.g., Emery 1988; Gulmon 1992; Keeley and Fotheringham 1998; Wall and Macdonald 2009) to better enable restorationists to collect and store high quality seed, and in turn reduce project costs and increase plant establishment (Barton et al. 2016).

Materials and Methods

This study was conducted with seed collected for restoration at Younger Lagoon Reserve (YLR) and Pinnacles National Park. YLR is a 29-hectare area of protected land (36.95370°N, –122.06654°W) adjacent to the Pacific Ocean that belongs to the University of

California Natural Reserve System and is dominated by coastal scrub and grassland habitat. Much of the site is currently being restored following a long history of agricultural land use. Seeds for the YLR study site were collected in Santa Cruz County along State Route 1 at Año Nuevo State Park (37.11931°N, –122.30765°W), Wilder Ranch State Park (36.96080°N, –122.08345°W), Coast Dairies State Park (36.98439°N, –122.15570°W), Scaroni Farms (36.97800°N, –122.13815°W), 4 mile Beach (36.96633°N , –122.12272°W), and the University of California at Santa Cruz (UCSC) at West Marshall Field (37.01869°N, –122.07562°W).

Pinnacles National Park (PNP) is a federally designated U.S. National Park about 65 km inland from the coast which includes chaparral, oak woodlands, and grassland ecosystems. Park staff are restoring a nearly flat 80.9-hectare degraded grassland near the east entrance to the park (36.49066°N, 121.18252°W). Seeds were collected at many sites within the boundaries of PNP.

We tested germination rates for 25 native perennial grass, forb, and shrub species that are commonly used for restoration at YLR and 9 native annual forb species that are being reintroduced to PNP (Appendix 1). Sixteen species from YLR were collected in 3–7 consecutive years (Appendix 1). Nine species from YLR and nine species from PNP were collected in 1 or 2 years (Appendix 1). Nomenclature throughout follows Jepson Flora Project (2019).

Seeds were collected from a minimum of 50 plants and at multiple sites, when possible, to ensure genetic diversity, following standard seed collection recommendations (Maschinski et al. 2012). The relative amount of seed of individual species collected from different sites varied annually depending on seed abundance at a given site. Seed collections from a given year were usually combined into one collection container after cleaning to conserve storage space. All seeds were initially stored in paper bags and air dried for 6–12 months. Seeds were then cleaned manually by passing seeds through a minimum of two mesh screens (0.074–3.8 mm) until the target seed was completely free of chaff. After cleaning, YLR seeds were primarily stored at ambient temperature, except for three species that were stored at –2°C (Appendix 1); all collections of individual species were stored at the same temperature. YLR species were stored in one-gallon plastic bags or paper envelopes (depending on volume), except for a few very-small seeded species in glass jars; most collections of the same species were stored in the same container type. All seeds from PNP were stored at ambient temperature in paper envelopes.

We conducted three rounds of germination testing at the Jean Langenheim Greenhouses, University of California, Santa Cruz. All PNP seed testing started on 13 January 2017; a small set of YLR seed was tested on 3 February 2017; and most YLR seeds, including species that were collected in ≥3 years, were tested starting 11–13 January 2018. All collections of the same species were tested in the same round, and each species was only tested during one round. For each species × collection year combination, 100 seeds were divided equally between four 10.16 × 10.16 × 15.24-cm pots filled with Pro-mix HP mycorrhizae soil. In each pot, 25 pre-cleaned, pre-counted seeds were placed into a 5 × 5 seed grid to avoid aggregation. We placed a light covering of soil over the seeds, approximately 1.5× the seed length. Pots were maintained at ambient temperature in a greenhouse receiving some indirect and some direct light. Pots were misted twice daily by the greenhouse irrigation system and watered additionally when the soil surface was dry to the touch. We monitored germination weekly for 11 weeks and removed all visible germinants from the soil with forceps cleaned with 70% alcohol solution to reduce microbial contamination.

For 2017 PNP seed testing, *Amsinckia menziesii* (Lehm.) A.Nelson & J.F.Macbr., *Calandrinia menziesii* (Hook.) Torr & A.Gray, *Castilleja exserta* subsp. *venusta* (A.Heller) T.I.Chuang & Heckard, *Clarkia unguiculata* Lindl., *Lasthenia gracilis* (DC.) Greene, and *Madia sativa* Molina were cold stratified at 2.78°C for 2–3 weeks (Emery 1988). For 2017 YLR seed testing, all seeds were initially placed in cold stratification without light at 2.78°C for five weeks and then moved to ambient temperature. No species were stratified in 2018 except for *Sisyrinchium bellum* S.Watson, which was stratified at 2.78°C for 6 weeks pre-sowing (Emery 1988).

ANOVA was used to evaluate whether the percent germination varied significantly among collection years for species that were collected in ≥3 years. When the effect of collection year was significant ($\alpha = 0.05$), we conducted Tukey's multiple comparison tests to compare individual years.

RESULTS

Germination rates varied greatly across species and collection year with 27 of the 34 species (76%), including all the annual species from PNP, exhibiting at least 25% germination in one or more collection years. No additional treatments were used to stimulate germination aside from stratification of several species as mentioned previously (Fig. 1, Table 1). *Artemisia californica* Less., *Frangula californica* (Eschsch.) A.Gray, and *Symphyotrichum chilense* (Nees) G.L.Nesom did not germinate, and *Carex gynodynama* Olney, *Danthonia californica* Bol., and *Sisyrinchium bellum* had ≤3% germination in all collection years. Of the 13 species that were collected over a period of ≥3 years that germinated, all but two showed significant interannual variation, and seven (54%) showed a trend of decreasing germination with increasing year since collection (Fig. 1, Appendix 2).

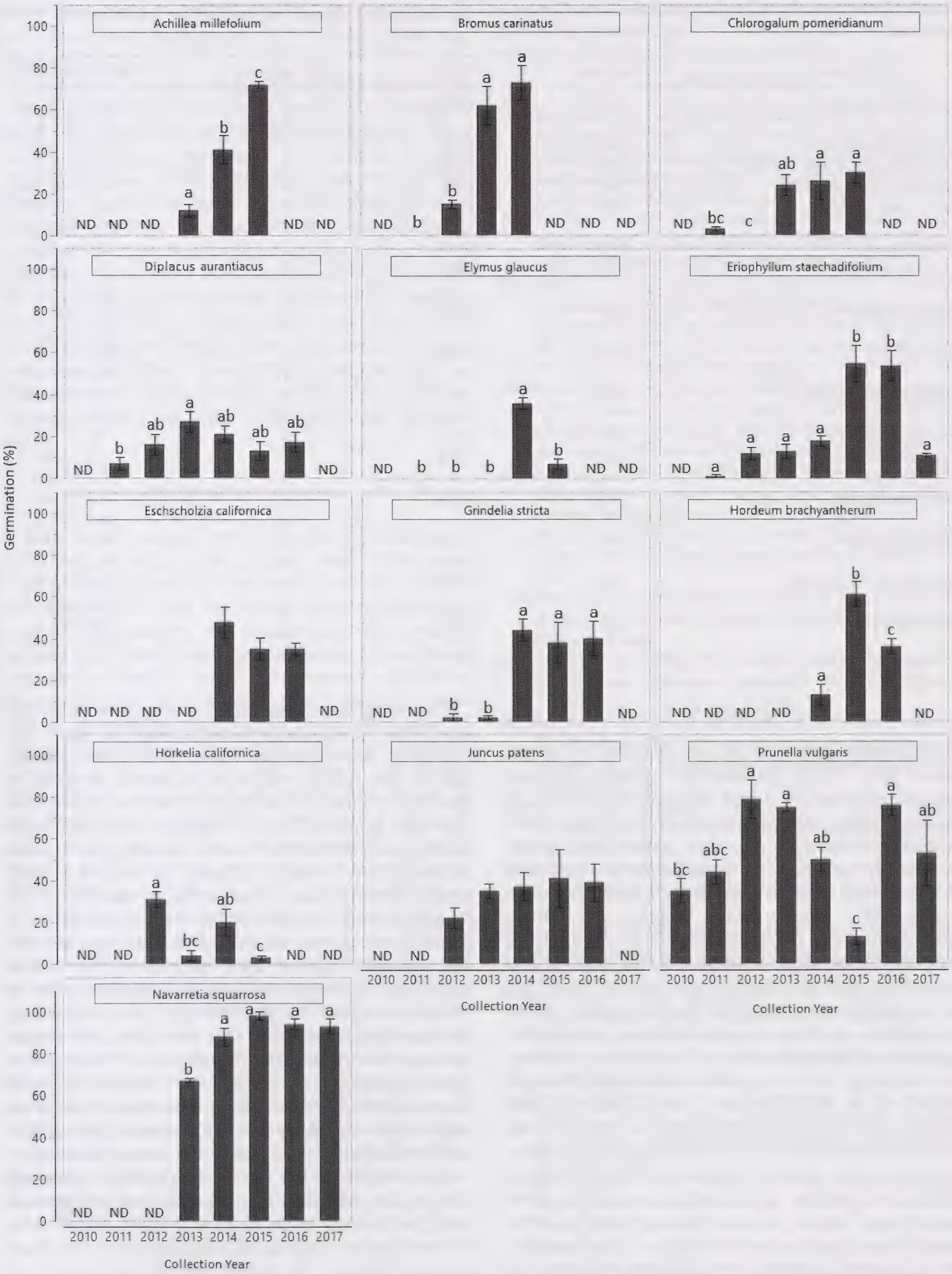

FIG. 1. Percent germination of species tested in ≥3 years. Error bars indicate 1 SD. When ANOVA (Appendix 2) indicated a significant effect of collection year on percent germination ($P < 0.05$), differences in means using Tukey's mean separation procedure are indicated with lower case letters. ND = no data for that collection year. All seeds were stored at ambient temperature, except *Achillea millefolium* Ledeb. and *Bromus sitchensis* var. *carinatus* which were stored at -2°C.

TABLE 1. PERCENT SEED GERMINATION OF ALL SPECIES COLLECTED IN 1 OR 2 YEARS. Values are mean germination percentages ± 1SD for n = 4.

Species	Test year	Site	Seed age (yr)	Germination (%)
Amsinckia menziesii	2017	PNP	1	84.0 ± 5.7
			5	76.0 ± 15.0
Calandrinia menziesii	2017	PNP	1	43.0 ± 24.1
Castilleja exserta ssp. *venusta*	2017	PNP	5	43.0 ± 6.0
Chaenactis glabriuscula	2017	PNP	1	79.0 ± 14.4
Clarkia unguiculata	2017	PNP	1	60.0 ± 19.9
			5	83.0 ± 11.9
Delphinium sp.	2017	PNP	1	94.0 ± 5.2
Lasthenia gracilis	2017	PNP	1	37.0 ± 6.0
			5	26.0 ± 6.9
Lupinus bicolor	2017	PNP	1	91.0 ± 3.8
			5	92.0 ± 3.3
Madia sativa	2017	PNP	1	85.0 ± 3.8
			5	58.0 ± 14.8
Cirsium quercetorum	2018	YLR	1	53.0 ± 11.0
			2	3.0 ± 3.8
Danthonia californica	2017	YLR	1	1.0 ± 2.0
Erigeron glaucus	2017	YLR	2	7.0 ± 3.8
			3	18.0 ± 8.3
Juncus mexicanus	2018	YLR	2	32.0 ± 10.3
			3	34.0 ± 9.5
Lupinus variicolor	2018	YLR	3	51.0 ± 10.0
			5	50.0 ± 5.2
Scrophularia californica	2017	YLR	2	57.0 ± 6.0
			5	74.0 ± 30.2
Stipa pulchra	2017	YLR	2	23.0 ± 8.2
			6	47.0 ± 11.9

DISCUSSION

Our results show that the vast majority of species studied had >25% germination without requiring seed pretreatment to break dormancy, despite the fact that many native species in California have complex germination triggers to ensure that germination only occurs when microclimatic conditions are favorable, such as sufficient rainfall and light (Keeley 1987; Emery 1988; Vaughn and Young 2010). While it is recommended to test viability of non-germinating seeds through a cut or crush test or tetrazolium chloride (Baskin and Baskin 2014), this was not possible for several of the tiny-seeded species we studied. A lack of appropriate germination triggers was likely the cause of little to no germination observed for *Sisyrinchium bellum* and *Frangula californica* in all collection years. Emery (1988) suggests 1.5 months stratification for newer seeds and no treatment for 3–6 year old seeds for *S. bellum*, and reports that stored *F. californica* seeds require at least three months of stratification. Also, some species may require two or more years of after-ripening to allow for gas exchange, water penetration, and neutralization of inhibitory chemicals to initiate germination events (Emery 1988; Baskin and Baskin 2014), a pattern consistent with the germination of *Eriophyllum staechadifolium* Lag. Likewise, Holl (unpublished data) observed that *S. bellum* germinated in the second year after sowing in another grassland restoration study near YLR.

Percent germination varied strongly by collection year. One explanatory factor could be seed age, consistent with previous studies, as approximately half of the species that were collected in three or more years showed a decrease in percent germination over time (Gulmon 1992; Tielbörger and Petrů 2010; Barton et al. 2016). Our results showing that *Bromus sitchensis* var. *carinatus* (Hook. & Arn.) R.E.Brainerd & Otting. and *Elymus glaucus* Buckley (both Poaceae) seeds are short lived when stored at room temperature are consistent with (Dremmen 2003) who reported seeds of those species only last around three years. Three of the four Asteraceae species we tested decreased in germination over time, and *Artemisia californica* seed that was three to five years old had low germination in all years. Observations from restoration efforts at the University of California, Santa Barbara concur that stored Asteraceae seeds tend to be short-lived (J. Luong, University of California, Santa Cruz, personal communication).

A number of other factors besides seed age could also explain the effect of collection year on germination, particularly given that the percent germination of four species (*Elymus glaucus*, *Hordeum brachyantherum* Nevski, *Horkelia californica* Cham. & Schltdl., and *Prunella vulgaris* L.) varied by collection year but showed no obvious directional trend. Past studies have shown that the rate of seed germination depends on initial seed quality and health of the parent population upon collection, which inevitably varies annually (Rajjou et al. 2008; Kochanek et al.

2011; Nguyen et al. 2012), often based on rainfall in the prior year (Kochanek et al. 2010; Zani and Müller 2017).

Collection practices may also partially explain the mixed germination trends we observed. Variation in local site conditions of the mother plant has been shown to explain germination variation in past studies (Gulmon 1992; Tielbörger and Petrů 2010). However, since PNP and YLR seed collections from different locations were pooled into one collection container to conserve space and labeled only with the collection year, we cannot tease out the separate effects of seed age and site on germination. Furthermore, the majority of seeds used in this study were stored in ambient temperature and moisture conditions, whereas best management practices call for storing seed at –20°C and low moisture conditions to maximize seed longevity (Linington and Manger 2014).

RECOMMENDATIONS

Our results suggest several recommendations for collecting, storing, and testing restoration seed stocks. First, in light of the species-specific rates of seed germination and the strong effect of collection year on germination, we recommend that restorationists test seed stock periodically to calibrate appropriate seeding rates and increase restoration success. Second, as a general rule of thumb, seeds should be used for restoration within a couple of years of collection to avoid potential reduced germination due to seed aging (Brown and Briggs 1991). Third, our results highlight the importance of collecting seed in multiple years and at multiple locations to ensure the greatest genetic diversity possible and to increase germination success (Emery 1988; Brown and Briggs 1991; Maschinski et al. 2012). Fourth, best management practices should be followed, such as labeling collections from different locations separately and cold storing seeds that will be held for multiple years (Maschinski et al. 2012). To date, most of the knowledge of seed germination triggers and longevity for California native species amassed by horticulturalists and restoration practitioners have not been widely disseminated. Hence, our final recommendation is for enhanced sharing of written documentation of successful and failed strategies in seed collection, storage, and sowing practices, which will enhance the success of native plant restoration throughout California.

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LITERATURE CITED

BARTON, M. L., I. D. MEDEL, K. K. JOHNSTON, AND C.R. WHITCRAFT. 2016. Seed collection and germination strategies for common wetland and coastal sage scrub species in southern California. Bulletin of the Southern California Academy of Sciences 115:41–71.

BASKIN, C. C. AND J. M. BASKIN. 2014. Seeds: ecology, biogeography, and evolution of dormancy and germination. Elsevier/Academic Press, San Diego, CA.

BROWN, A. H. D. AND J. D. BRIGGS. 1991. Sampling strategies for genetic variation in ex situ collections of endangered plant species. Pp. 99–119 *in* D. A. Falk and K. E. Holsinger (eds.). Genetics and conservation of rare plants. Oxford University Press, New York, NY.

DICKIE, J. B., K. H. GAJJAR, P. BIRTCH, AND J.A. HARRIS. 1988. The survival of viable seeds in stored topsoil from opencast coal workings and its implications for site restoration. Biological Conservation 43:257–265.

DREMANN, C. 2003. Observations on *Bromus carinatus* and *Elymus glaucus* seed storage and longevity. Native Plants Journal 4:61–64.

EMERY, D. E. 1988. Seed propagation of native California plants. Santa Barbara Botanic Garden, Santa Barbara, CA.

FENNER, M. 2017. Ecology of seed banks. Pp. 507–528 *in* J. Kigel (ed.). Seed development and germination. Routledge, London.

GULMON, S. L. 1992. Patterns of seed germination in Californian serpentine grassland species. Oecologia 89:27–31.

HOEKSTRA, J. M., T. M. BOUCHER, T. H. RICKETTS, AND C. ROBERTS. 2005. Confronting a biome crisis: global disparities of habitat loss and protection. Ecology Letters 8:23–29.

JEPSON FLORA PROJECT (eds.) [2019] Jepson eFlora. Website: https://ucjeps.berkeley.edu/eflora/ [accessed on Feb 23 2020].

KEELEY, J. E. 1987. Role of fire in seed germination of woody taxa in California chaparral. Ecology 68:434–443.

——— AND J. FOTHERINGHAM. 1998. Smoke-induced seed germination in California chaparral. Ecology 79:2320–2336.

KOCHANEK, J., K. J. STEADMAN, R. J. PROBERT, AND S. W. ADKINS. 2011. Parental effects modulate seed longevity: exploring parental and offspring phenotypes to elucidate pre-zygotic environmental influences. New Phytologist 191:223–233.

———, Y. M. BUCKLEY, R. J. PROBERT, S. W. ADKINS, AND K. J. STEADMAN. 2010. Pre-zygotic parental environment modulates seed longevity. Austral Ecology 35:837–848.

LININGTON, S., AND K. MANGER. 2014. Seed bank design: cold rooms for seed storage. Technical Information Sheet 12. Millenium Seed Bank Project, Royal Botanic Gardens, Kew, UK. Website: https://www.kew.org/sites/default/files/12-Cold%20room%20design%20web.pdf. [acccessed 25 March 2019].

MASCHINSKI, J., M. A. ALBRECHT, L. MONKS, AND K. E. HASKINS. 2012. Center for Plant Conservation best reintroduction practice guidelines. Pp. 277–306 *in* J. Maschinski and K. E. Haskins (eds.). Plant reintroduction in a changing climate: promises and perils. Island Press, Washington, DC.

NGUYEN, T. P., P. KEIZER, F. VAN EEUWIJK, S. SMEEKENS, AND L. BENTSINK. 2012. Natural variation for seed longevity and seed dormancy are negatively correlated in *Arabidopsis*. Plant Physiology 160:2083–2092.

PRIESTLEY, D., V. CULLINAN, AND J. WOLFE. 1985. Differences in seed longevity at the species level. Plant, Cell, and Environment 8:557–562.

RAJJOU, L., Y. LOVIGNY, S. P. C. GROOT, M. BELGHAZI, C. JOB, AND D. JOB. 2008. Proteome-wide characterization of seed aging in *Arabidopsis:* A comparison between artificial and natural aging protocols. Plant Physiology 148:620–641.

STROMBERG, M. R., C. M. D'ANTONIO, T. P. YOUNG, J. WIRKA, AND P. R. KEPHART. 2007. California grassland restoration. Pp. 254–280 *in* M. R. Stromberg, J. D. Corbin, and C. M. D'Antonio (eds.). California Grasslands. University of California Press, Berkeley, CA.

TIELBÖRGER, K., AND M. PETRŮ. 2010. An experimental test for effects of the maternal environment on delayed germination. Journal of Ecology 98:1216–1223.

VASEY, M. C., AND K. D. HOLL. 2007. Ecological restoration in California: challenges and prospects. Madroño 54:215–224.

VAUGHN, K. J., AND T. P. YOUNG. 2010. Contingent conclusions: year of initiation influences ecological field experiments, but temporal replication is rare. Restoration Ecology 18:59–64.

WALL, M. AND J. MACDONALD. 2009. Processing seeds of California native plants for conservation, storage, and restoration. Rancho Santa Ana Botanical Garden Occasional Publication, Number 10. Claremont, CA.

WALTERS, C., L. M. WHEELER, AND J. M. GROTENHUIS. 2005. Longevity of seeds stored in a genebank: species characteristics. Seed Science Research 15:1–20.

WANG, Z., L. WANG, Z. LIU, Y. LI, Q. LIU, AND B. LIU. 2016. Phylogeny, seed trait, and ecological correlates of seed germination at the community level in a degraded sandy grassland. Frontiers in Plant Science 7:1532–1540.

WULFF, R. 1995. Environmental maternal effects on seed quality and germination. Pp.491–506 *in* J. Kigel and G. Galili (eds.). Seed development and germination. Marcell Dekker, Inc. New York, NY.

ZANI, D., AND J. V. MÜLLER. 2017. Climatic control of seed longevity of *Silene* during the post-zygotic phase: do seeds from warm, dry climates possess higher maturity and desiccation tolerance than seeds from cold, wet climates? Ecological Research 32:983–994.

APPENDIX 1. SPECIES TESTED IN 2017 AND 2018 GERMINATION TESTS. Species marked with "*" were species that were collected over a period of ≥ 3 years and tested in 2018.

Latin name	Common name	Growth form	Site	Collections tested in		Storage temperature
				2017	2018	
Amsinckia menziesii	Menzies' fiddleneck	annual forb	PNP	2012, 2016		ambient
Calandrinia menziesii	redmaids	annual forb	PNP	2016		ambient
Castilleja exserta subsp. *venusta*	purple owl's clover	annual forb	PNP	2012		ambient
Chaenactis glabriuscula DC	yellow pincushion	annual forb	PNP	2016		ambient
Clarkia unguiculata	elegant clarkia	annual forb	PNP	2012, 2016		ambient
Delphinium sp.	larkspur	annual forb	PNP	2016		ambient
Lasthenia gracilis	goldfield	annual forb	PNP	2012, 2016		ambient
Lupinus bicolor Lindl.	miniature lupine	annual forb	PNP	2012, 2016		ambient
Madia sativa	coast tarweed	annual forb	PNP	2012, 2016		ambient
Bromus sitchensis var. *carinatus*	California brome	perennial graminoid	YLR		2011–2014, *	–2°C,
Carex gynodynama	Olney's hairy sedge	perennial graminoid	YLR		2015, 2016	ambient
Danthonia californica	California oatgrass	perennial graminoid	YLR	2016		ambient
Elymus glaucus	blue wild rye	perennial graminoid	YLR		2011–2015, *	–2°C
Hordeum brachyantherum	meadow barley	perennial graminoid	YLR		2014–2016, *	2014–2016 ambient
Juncus mexicanus Willd.	Mexican rush	perennial graminoid	YLR		2015, 2016	ambient
Juncus patens E.Mey	California grey rush	perennial graminoid	YLR		2012–2016, *	ambient
Stipa pulchra Hitchc.	purple needlegrass	perennial graminoid	YLR	2011, 2015		ambient
Eschscholzia californica Cham.	California poppy	annual/perennial forb	YLR		2014–2016, *	ambient
Achillea millefolium	common yarrow	perennial forb	YLR		2013–2015, *	–2°C
Chlorogalum pomeridianum Kunth	California soaproot	perennial forb	YLR		2011–2015, *	ambient
Cirsium quercetorum Jeps.	brownie thistle	perennial forb	YLR		2016, 2017	ambient
Erigeron glaucus Ker Gawl.	seaside daisy	perennial forb	YLR		2015, 2016	ambient
Grindelia stricta DC.	Oregon gumplant	perennial forb	YLR		2012–2016, *	ambient
Horkelia californica	California horkelia	perennial forb	YLR		2012–2015, *	ambient
Navarretia squarrosa (Eschsch.) Hook. & Arn.	skunkweed	perennial forb	YLR		2013–2017, *	ambient
Prunella vulgaris	self-heal	perennial forb	YLR		2010–2017, *	ambient
Scrophularia californica Cham. & Schltdl.	California bee plant	perennial forb	YLR	2012, 2015		ambient
Sisyrinchium bellum	blue-eyed grass	perennial forb	YLR		2013–2016, *	ambient
Symphyotrichum chilense	California aster	perennial forb	YLR	2012, 2016		ambient
Artemisia californica	California sagebrush	shrub	YLR		2013–2015, *	ambient
Diplacus aurantiacus (Curtis) Jeps.	sticky monkeyflower	shrub	YLR		2011–2016, *	ambient
Eriophyllum staechadifolium	lizard tail	shrub	YLR		2011–2017, *	ambient
Frangula californica	California coffeeberry	shrub	YLR		2013–2016, *	–2°C
Lupinus variicolor Steud.	many colored lupine	shrub	YLR		2013, 2015	ambient

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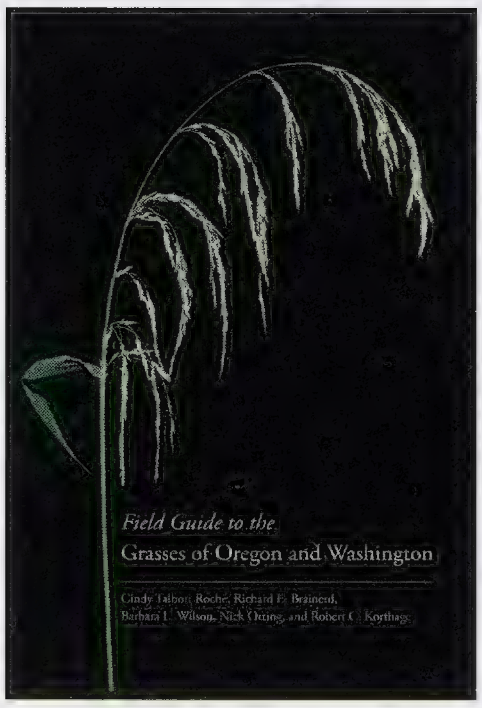
Book Review


Field Guide to the
Grasses of Oregon and Washington
Cindy Talbott Roché, Richard E. Brainerd,
Barbara L. Wilson, Nick Otting, and Robert C. Korfhage

Field Guide to the Grasses of Oregon and Washington. By CINDY TALBOTT ROCHÉ, RICHARD E. BRAINERD, BARBARA L. WILSON, NICK OTTING, AND ROBERT C. KORFHAGE. 2019. Oregon State University Press, Corvallis, Oregon. 460 pp. ISBN 978-0870719592 (paperback). Price: $35.00, paperback edition.

This field guide to all of the grasses (except bamboos) that grow outside cultivation in Oregon and Washington includes 376 taxa. The book has five sections: an introduction (14 pages), keys to genera and species (75 pages), and species accounts with color photos, description and distribution map (346 pages), followed by a glossary and index. Why am I reviewing it for California botanists? Because California botanists will find this book a valuable supplement to our own field guides to grasses. Many of the grasses that grow in Oregon and Washington also grow in California, ranging from widespread native and introduced species to even some rare species. You would not expect to find California's rare endemic species, *Agrostis blasdalei* Hitchc., in the field guide, but much to our surprise, it was recently found on the southern Oregon coast. (Of course, it is no longer a California endemic). Some California serpentine and alpine and subalpine grasses are also well described and illustrated in this guide. It does not include all California grasses; California has habitats not well represented in the Pacific Northwest, such as vernal pools, chaparral, and hot southern deserts, and, therefore, supports a greater diversity of species. Nevertheless, no treatment of California grasses is better illustrated or as up-to-date as this field guide (other than the *Flora of North America*; Barkworth et al. 2003, 2007).

People have developed many ways to use field guides to identify a grass in hand: some go right to a key, while others leaf through pictures looking for something similar. Most of us prefer to ask someone who knows grasses, but let's say we're on our own with only a field guide. Where to start, what features to examine first, how to tell that it is indeed a grass and not a rush or sedge? The introduction meets our needs at this initial stage. The authors, whose extraordinary talents brought this exceptional field guide to fruition, note that many plants with common names that include the word "grass" are not grasses; for example, bear grass (*Xerophyllum tenax* (Pursh) Nutt.) is not a grass. Then, they distinguish grasses from other graminoids, like sedges and rushes, describing the differences in stem and flower characters. For example, sedge flowers are protected by one bract while grass flowers are enclosed by two bracts: the lemma and palea. The introduction also includes a section entitled "Grass Structure and Vocabulary," which is as important as the emphatic "READ ME" next to the title indicates. You can't use the key if you don't know the terminology used in grass anatomy. You'll return frequently to these pages as you work the key and in time you will become fluent in the vocabulary. The vegetative structures are well described, often with practical suggestions. For example, flowers (also known as florets) are arranged in spikelets that are subtended by two additional bracts, called glumes. Spikelet compression can be detected by laying a spikelet on a tabletop. If both glumes are visible, it is *laterally* compressed. If only one glume is visible, it is *dorsiventrally* compressed. If it takes a variety of positions, it is probably not compressed; it is cylindrical or *terete*. In my opinion, the authors could have beefed up this section on structure and vocabulary with more drawings, or they could have illustrated the glossary. Since this section of the guide should address the needs of the beginner, it would have been useful to include definitions and, preferably, illustrations of *all* the technical words used in the key and species treatments. I selected a couple of species treatments randomly to test this notion and, although most of the descriptive words are defined either in the "Vegetative Structures" section or in the glossary, the very first species treatment I turned to, on page 148, used a word undefined anywhere: "scurfy." To address this deficiency, I will paste an illustrated glossary from another source on the inside back cover of my copy.

Well-written keys, like those here, will deliver the answer 90% of the time, but they aren't perfect nor are their users. Characters in keys usually describe mature, complete plants, but specimens are frequently incomplete, immature, or senescent; the authors thus recommend collecting multiple specimens. If you reach a dead end following one lead, go back and follow the other lead. If that doesn't work, go back one step more and try again. The authors of the keys are veterans of the *Carex* Working Group, who published a field guide to sedges for the Pacific Northwest and also wrote the graminoid keys for the *Flora of Oregon* and the *Flora of the Pacific Northwest* (Meyers et al. 2015; Hitchcock and Cronquist 2018). They note that users will learn from experience that some characters are generally more reliable than others, that some grasses favor particular habitats, and how to visualize the characters in the descriptions. The emphasis on learning over time suggests that keying grasses requires patience, that even experienced naturalists find grasses challenging.

The descriptions of species are generous in technical detail. Photographs of a whole plant, its habitat, inflorescence and details of the spikelet and seeds accompany most of the species treatments. The photographs are excellent both in quality and content, and they supplement the key and the verbal descriptions handsomely, clarifying fine points and generally improving the likelihood of successful identification. They answer a frequent prayer of those of us who often find verbal descriptions insufficiently descriptive: "oh, please, show me a picture of that feature!!"

The shortcomings I mentioned are exceptions in an otherwise splendidly comprehensive treatment of the grasses of Oregon and Washington, a book I will take with me wherever I go in the Pacific Northwest and will supplement my efforts in grass identification in California.

This field guide will be useful long into the future. Even after climate change leaves its awful marks on the landscape and taxonomists find reason to change all the grass names again, the images and descriptions will connect the changes to what you see in the field. While California botanists should consult local keys to avoid overlooking species not found in Oregon and Washington, this book is worth buying for the images and descriptions, serving as an invaluable supplement to any California flora or field guide.

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LITERATURE CITED

BARKWORTH, M. E., K. M. CAPELS, S. LONG, L.K. ANDERTON, AND M. B. PIEP (eds.). 2007. *In* Flora of North America Editorial Committee (eds.), Flora of North America, North of Mexico, vol. 24: Magnoliophyta: Commelinidae (in part): Poaceae, Part 1. Oxford University Press, New York, NY.

BARKWORTH, M. E., K. M. CAPELS, S. LONG, L. K. ANDERTON, AND M. B. PIEP (eds.). 2003. *In* Flora of North America Editorial Committee (eds.), Flora of North America, North of Mexico, vol. 25: Magnoliophyta: Commelinidae (in part): Poaceae, Part 2. Oxford University Press, New York, NY.

HITCHCOCK, C. L. AND A. CRONQUIST. 2018. Flora of the Pacific Northwest: an illustrated manual. Second Edition. D.E, Giblin, B.S. Legler, P.F. Zika, and R.G. Olmstead (eds.). University of Washington Press, Seattle, WA.

MEYERS, S. C., T. JASTER, K. E. MITCHEL, L. K. HARDISON (eds.). 2015. Flora of Oregon. Vol. 1, Pteridophytes, Gymnosperms, and Monocots. Journal of the Botanical Research Institute of Texas. Fort Worth, TX.

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CORRIGENDUM

CORRECTION TO "*SILENE NELSONII*, A NEW LARGE-FLOWERED SPECIES FROM THE TRINITY RIVER AREA OF NORTHWESTERN CALIFORNIA, USA, AND A RE-EVALUATION OF *S. BOLANDERI* GRAY"

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Due to transcription errors, the spatial coordinates presented in the Paratypes section are incorrect. A revised version of this section is presented below.

Paratypes (arranged alphabetically by collector within county. Note: locality information, including spatial coordinates (NAD 83), is provided only when given on the collection label.): USA., CALIFORNIA, **Humboldt County**: Brush Mountain, 26 May 1983, *Jimerson sn* (CAS); FS 5N40 about 3.2 miles from NF 60, 40.76532, –123.51479, 4092 ft, 3 Jun 2013, *Mesler 1481* (HSC); FS 6, 1 mile south of Sims Mtn, 40.72484, –123.60366, 3600 ft, 5 May 2018, *Mesler 1665a* (HSC); FS 6 near Manzanita Ranch, 40.71958 –123.54644, 1680 ft, 19 May 2018, *Mesler 1667* (HSC); Friday Ridge Road, near intersection with Hwy 299, 7 May 1978, *Reed 45* (HSC); Brannan Mountain, 4000 ft, 7 July 1911, *Tracy 3414* (UC); **Shasta County**: Basin Gulch Camp, 40.35413, –122.96176, 2570 ft, 4 May 2013, *Mesler 1476* (HSC); **Trinity County**: Burnt Ranch USFS campground, 412 m, 30 April 1983, *Janeway 245* (HSC); Weaverville, *Kleeberger sn* (CAS); Hyampom Rd, west of Hayfork, 40.57720, –123.25116, 2100 ft, 7 June 2011, *Mesler 850* (HSC); Wildwood Rd, near Gemmill Gulch, 40.43464, –123.05697, 3290 ft, 30 May 2010, *Mesler 818* (HSC);Weaverville, Garden Gulch Trail, 40.75234, –122.94912, 2300 ft, 7 June 2010, *Mesler 821* (HSC); North of Hyampom along NF 60, 40.57954, –123.25527, 2300 ft, 29 May 2011, *Mesler 846* (HSC); south of Indian Valley Guard Station along NF 7, 40.46557, –123.29167, 4000 ft, 8 Jun 2011, *Mesler 852* (HSC); North of Indian Valley Guard Station on NF 10, 40.53945, –123.34832, 4050 ft, 8 Jun 2011, *Mesler 853* (HSC); Philpot Camp near Peanut, 40.46500 –123.19028, 2600 ft, 26 May 2013, *Mesler 1479* (HSC); FS 30N01 near Wildwood, 40.40018, –123.00084, 4380 ft, 26 May 2013, *Mesler 1480* (HSC); Ewing Reservoir, Hayfork, 40.56443, –123.16867, 2440 ft, 20 May 2018, *Mesler 1671* (HSC); south of Wildwood on FS29N28, 40.36220, –123.07039, 4100 ft, 27 Jun 2018, *Mesler 1690* (HSC); FS 60 6.6 mi south of Hwy 299, 3500 ft, 30 May 1980, *Nelson 5347* (HSC); FS 60 10 mi south of Hwy 299, 4400 ft, 30 May 1980, *Nelson 5360* (HSC); 2 miles east of Burnt Ranch, 16 Jun 1964, *Spellenberg 438* (HSC); east side of Underwood Mtn Rd (5N09), ca. 4.9 miles south of Hwy 299, 12 June 1980, *Taylor 2855* (CHSC); near summit of Hayfork Mountain on Weaverville Rd, 30 June 1923, *Tracy 6444* (UC); Burnt Ranch, 1500 ft, 27 April 1924, *Tracy 6655* (UC); north of Philpot campground, 2600 ft, 13 May 1979, *York 286* (HSC).

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